CHAPTER 7-1

WATER RELATIONS: CONDUCTING STRUCTURES

TABLE OF CONTENTS

Movement to Land 7-1-2
Bryophytes as Sponges 7-1-2
Conducting Structure 7-1-4
Leptomes and Hydromes 7-1-8
Hydroids 7-1-12
Leptoids 7-1-14
Rhizome 7-1-15
Leaves 7-1-15
Costa 7-1-16
Sphagnum 7-1-17
Leafy Liverworts 7-1-17
Leaf Traces 7-1-18
Sporophyte Conduction 7-1-19
Adaptation and Evolution 7-1-21
Being Acrocarpous 7-1-21
Being Pleurocarpous 7-1-22
Aquatic 7-1-23
Using a Partner 7-1-24
Summary 7-1-25
Acknowledgments 7-1-26
Literature Cited 7-1-26

CHAPTER 7-1

WATER RELATIONS: CONDUCTING STRUCTURES

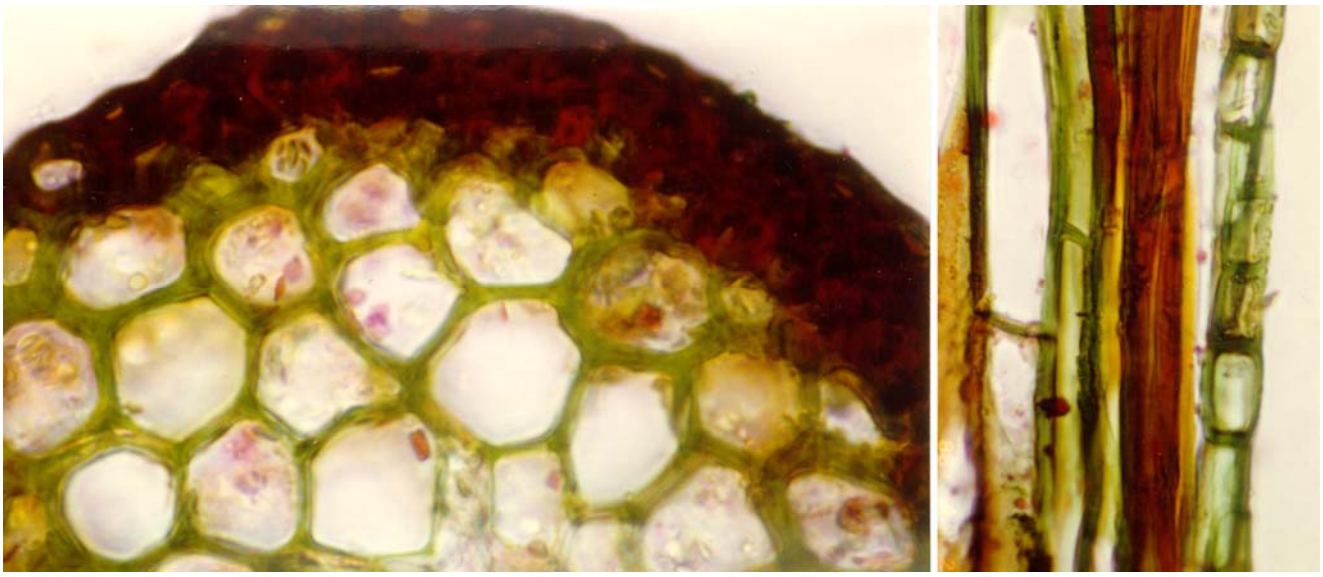

Figure 1. Cross section (**left**) and longitudinal section (**right**) of the moss ***Bryoxiphium***, showing in vertical section how cells that appear in cross section to be only parenchyma cells may in fact be elongate cells suitable for conduction. Photo courtesy of Isawo Kawai.

Movement to Land

The most obvious need for photosynthetic organisms in their move from water to land was the continued need for water. At this time, most photosynthetic organisms still had a dominant gametophyte, and all indications are that the movement onto land carried with it that gametophytic dominance. As life on land progressed through evolution, plants with sophisticated vascular tissue ultimately developed. At the same time, the gametophyte in these highly vascularized tracheophytes (lignified vascular plants) solved its water problems by ultimately being contained within the protection of sporophytic tissues in the seed plants.

This reduction of the gametophyte might necessarily have forced a reduction in conducting tissues because the surrounding sporophytic tissue on the one hand reduced available space and on the other made vascularization much less necessary in the gametophyte. But in gametophyte-dominant bryophytes, survival on land required a means for getting water, and the nutrients carried with it, from one part of the plant to another. Despite their being the first land plants, as Raven (2002) has put it, plant biologists have taken a "top-down" view of land plants, seemingly expecting the bryophytes to have a simpler version of the same system as tracheophytes.

But bryophytes have been around much longer than tracheophytes, and their gametophytes have remained dominant. Hence, should we not expect them to have evolved means of water movement in the gametophyte generation during all these millennia? First of all, consider the desiccation-tolerant tracheophytes. These are almost all small plants (Raven 2002). Many bryophytes are likewise desiccation tolerant, and they too are small.

Bryophytes as Sponges

Sponges, both animal and synthetic, gain and retain water through small chambers and capillary spaces. Bryophytes, due to their small size and tiny leaves, are natural arrays of chambers and capillary spaces. As this story unfolds, you will soon see that bryophytes are indeed sponges, aiding their own water needs and in some cases massively affecting the **ecosystem** (interacting community & habitat).

All life needs water, and the most severe stress for organisms venturing onto land was undoubtedly just that. But already, algae had developed means of becoming dormant through zygospores when they faced unfavorable circumstances. However, those first land organisms had to find ways to get water to all their internal parts, and often this water was in very limited amounts. For bryophytes, surviving water loss and prolonged periods of drought was a necessity for survival, so it is not surprising that during their 450 million years of evolutionary history (Proctor 2000a) they have perfected physiological mechanisms that

outdistance those of their tracheophyte counterparts (Oliver *et al*. 2000a). This ability has led plant physiologists to use bryophytes as model systems for the study of desiccation tolerance physiology, even to the extent of attempting to introduce those genes to crop plants (Comis 1992; Oliver *et al*. 2000b). And this use has made it into the agricultural literature with articles such as "Miracle Moss" (Comis 1992).

It appears that despite the typical relegation of bryophytes to the category of "non-vascular," conduction has played a major role in the phylogenetic history of bryophytes. Hedenäs (1999) examined the importance of various character states on the phylogenetic history of **pleurocarpous** mosses (typically the ones that grow horizontally) and determined that, based on redundancy analysis, gametophyte variance relates to characters associated with water conduction. Furthermore, one of the most important environmental variables in this phylogeny was the non-wetland to wetland gradient. On the other hand, Proctor (2000b), in "The bryophyte paradox: Tolerance of desiccation, evasion of drought," points out that a desiccation-tolerant tree is hardly conceivable. Height necessitates highly developed conducting systems that are unnecessary in short plants, and even among the bryophytes, it is the tall ***Dawsonia*** (Figure 2) and ***Polytrichum*** (Figure 3-Figure 4) that have conducting systems that almost mimic those of **tracheophytes** (plants having tracheids, *i.e.* the lignified vascular plants).

Figure 2. ***Dawsonia***, one of the tallest and most highly structured of all mosses. Photo by Janice Glime.

Ecosystem processes cannot be understood without understanding the role of bryophytes and their water relations. A lack of understanding of bryophyte water relations has led ecologists to conduct inappropriate experiments or draw erroneous conclusions about such topics as nutrient cycling and effects of air-borne pollutants on mosses in general in the ecosystem. Mosses such as ***Polytrichum*** (Figure 3-Figure 4), among the most conductive bryophytes in the northern hemisphere, have been used to generalize about the behavior of soil and airborne minerals in mosses during ecosystem processes. But this moss can behave very differently from most of the other genera that carpet forest floors. Puckett (1988) warns that mosses with internal conduction (as in ***Polytrichum***) do not make good monitors. Anderson and Bourdeau (1955) concluded that dew and rain were the main sources of water for bryophytes, excluding the groundwater source so vital for tracheophytes. It is therefore important that ecosystem ecologists, especially those studying water relations and nutrient cycling, have a basic understanding of the variety of ways that bryophytes move water and nutrients.

Figure 3. ***Polytrichum commune*** with capsules 1 Kristian Peters, through Creative Commons.

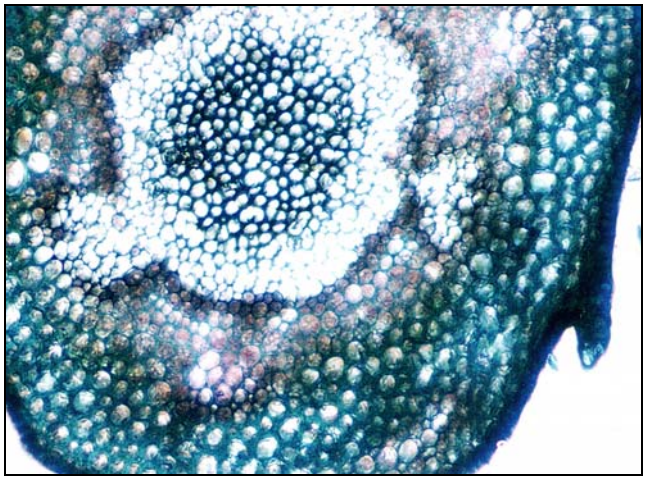

Figure 4. ***Polytrichum*** stem cross section showing central hydrome and surrounding leptome – the essence of its vascular system. Photo courtesy of Isawo Kawai.

Nearly every botany book on the market defines bryophytes as non-vascular plants, distinguishing them in this way from all other embryophytes. In fact, **many bryophytes are vascular**, but **lacking lignin** [associated with cellulose in cell walls of **sclerenchyma** (thick-walled supporting cells), xylem vessels, and tracheids; Hébant 1977] and the variety of perforated and spirally thickened cells typical of xylem. Rather, many bryophytes have unique cells that perform conduction in rather different

ways from the "true vascular plants." Kawai has published a series of colored photographs (*e.g.* Figure 1), using specific stains, that illustrate the wide presence and variety of such tissues among many families of mosses (Kawai 1971a, b, c, 1976, 1977a, b, 1978, 1979, 1980a, b, 1981, 1982, 1989, 1991a, b; Kawai & Ikeda 1970; Kawai & Ochi 1987; Kawai *et al*. 1985, 1986; Ron & Kawai 1990). Hence, it is safer to distinguish the bryophytes as non-lignified plants (still waiting to be disproved) or **non-tracheophytes**, and the lignified vascular plants as **tracheophytes**. This puts a slightly new perspective on the way we look at their roles in ecosystems.

When we consider bryophytes, we are tempted to think about wet habitats where mosses grow close to water, basking in the sun of a bog, or cooling off in the spray of a waterfall. Certainly these are habitats where bryophytes are common, but keep thinking. What about those rocks on the cliff or the sand of the dunes (Figure 5)? In fact, can you think of any habitat that has plants but where it is impossible to find mosses? There are not many, and if you visualize some of the rocky habitats in your mind, you realize that these organisms undergo tremendous changes in moisture and temperature, even within a single day, occupying habitats where no vascular plants can survive.

Figure 5. ***Aloina ambigua*** growing in sand. Photo by Michael Lüth, with permission.

If we try to speculate about those first organisms to survive on land, we would probably consider them to be simple organisms with no organized vascular systems. There was no selection pressure for any wasteful vascular tissue while these organisms were living in the water. Water may have been the primary force limiting plants from vast colonization of land. Gray (1985) suggests that it was the ecophysiological tolerance to desiccation, appropriate life cycle strategies, and short vegetative life cycle that permitted widespread colonization during the mid **Ordovician** (~441-504 million years ago) to the mid Early Silurian (~400-440 million years ago) – strategies that describe bryophytes.

Even with so many diverse habitats occupied by plants today, we still consider the move from water to land to have been a major one. Imagine the changes that were necessary. Consider that the greatest overriding challenge was to keep their cells wet. Land plants responded to this challenge in two ways. Some, the ones we traditionally called **vascular plants** (the **tracheophytes**), acquired **lignin**, developed a complex water transport system, and encased themselves in a waxy, waterproof **cuticle**. Others, the **bryophytes**, developed strategies that we are only beginning to understand, including external transport, cell-to-cell transport, and the ability to survive desiccation. In the words of Proctor (2000a), "Bryophytes... evolved desiccation tolerance and represent an alternative strategy of adaptation to life on land, photosynthesizing and growing when water is available, and suspending metabolism when it is not. Limited by mode of life, but also liberated: prominent on hard substrates such as rock and bark, which are impenetrable to roots and untenable to vascular plants. Bryophytes (in species numbers the second biggest group of green land plants) may be seen as mobile phones, notebook computers and diverse other rechargeable battery-powered devices of the plant world – not direct competitors for main-based equivalents, but a lively and sophisticated complement to them."

Bryophytes are adapted to land but restricted in their morphology by a biochemical impasse, *i.e.* the inability to synthesize lignin (Niklas 1976). Because they lack lignin, they lack the tracheids and vessels of other plants, but have produced instead vascular strands with similar elongate shapes. Nevertheless, they are unable to support a large structure or great mass because they lack the strengthening ability of lignin. Because of their importance in both structure and physiology, water relations seem an appropriate place to start in our consideration of the limits imposed on bryophytes, for without that understanding, we cannot understand their other limitations, nor can we fully evaluate their ecological relationships.

Conducting Structure

Conducting structures are not new expressions in bryophytes. Edwards *et al*. (2003) found at least fourteen types of such structures in mesofossils from a Lochkovian (Lower Devonian) locality in the Welsh Borderland, Shropshire. These are distinguished by variation in the combination of cells in the central strand and the cell wall architecture. The elongate cells may have smooth, uniformly thick or thin walls, walls with smooth projections pointed inward, or bilayered walls. The innermost walls are perforated by pores with the dimensions of plasmodesmata. These perforations are not well organized and some resemble the secondary thickenings most similar to the S-type tracheids of the **Rhyniopsida** (Figure 6-Figure 7), a primitive tracheophyte with lignified vascular tissue. Edwards and coworkers suggest that the imperforate bilayered examples may have been used in water conduction, cells that exhibited globular residues may have facilitated metabolite movement, and smooth-walled elongate cells seemed to be involved in support. They were unable to identify these mesofossils to genus, but concluded that there was widespread anatomical diversity among these early bryophytes.

Broadly speaking, imperforate bilayered examples may have been involved in water conduction, cells with globular residues with or without pitting involved in metabolite movement, and smooth-walled examples with or without projections involved in support.

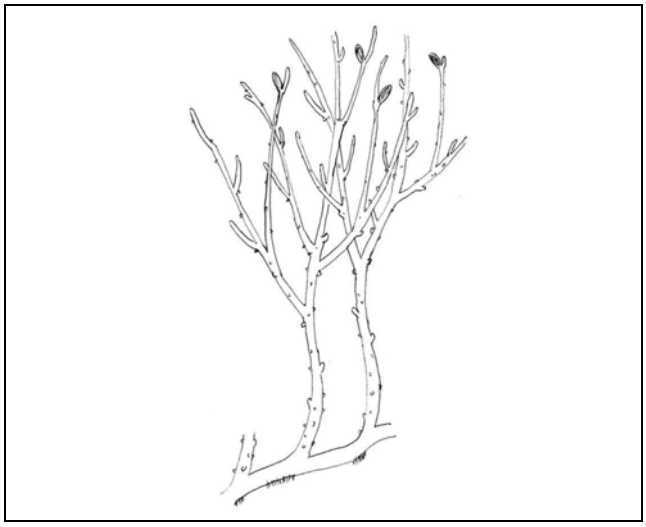

Figure 6. ***Rhynia gwynne-vaughanii*** reconstruction, member of **Rhyniophyta** – an early vascular plant. Photo by Griensteidl, through Creative Commons.

Bryophytes have two paths of water movement, often both in the same plant: internal through a **central cylinder** (**endohydric**) and external along the surface of the leafy or thallose plant (**ectohydric**) (Buch *et al*. 1938). Some thallose liverworts, **Polytrichaceae**, and **Mniaceae** represent the endohydric groups (Buch 1945, 1947; Proctor 2000b), but there are many others with at least some internal conduction. ***Metzgeria furcata*** (Figure 8), a "thallose" liverwort in the **Jungermanniopsida**, and others in the **Marchantiopsida**, have midribs (Figure 9) with enlarged internal cells (Figure 10), but the relative importance of these midrib cells for conduction is largely unknown.

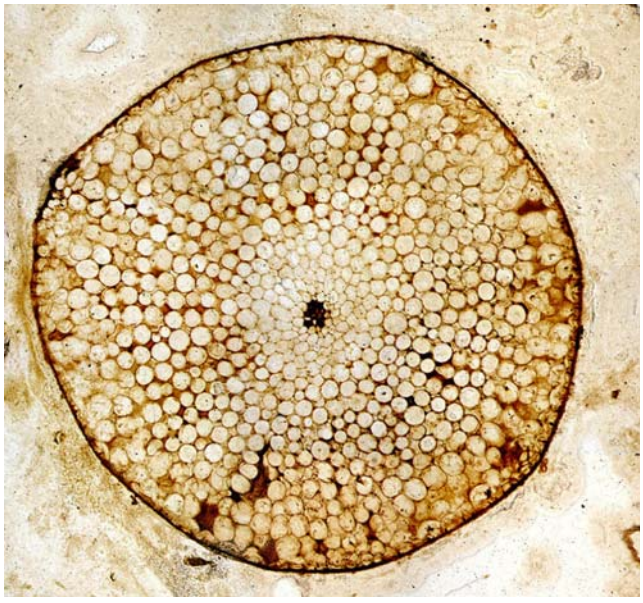

Figure 7. ***Rhynia gwynne-vaughanii*** stem cs fossil. Photo by Plantsurfer, through Creative Commons.

In liverworts, conducting tissues are restricted to the gametophyte, whereas in mosses, they are sometimes also in the sporophyte (Ligrone *et al*. 2000). Among the liverworts, the **Calobryales** and **Pallaviciniaceae** in the **Metzgeriales** have water-conducting cells with walls perforated by pores derived from plasmodesmata. The **hydroids** (water-conducting cells) of bryoid mosses are imperforate. In the **Polytrichaceae**, there is an axial system of microtubules in the **leptoids** (food-conducting cells) and in the parenchyma cells of the stems and setae of other mosses such as ***Sphagnum***, representing the variety of expression of conducting cells in the bryophytes..

Figure 8. ***Metzgeria furcata*** thallus with midrib. Photo by Des Callaghan, with permission.

Figure 9. ***Metzgeria furcata*** thallus showing distinct midrib with elongated cells and one layer of parenchyma cells in the thallus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

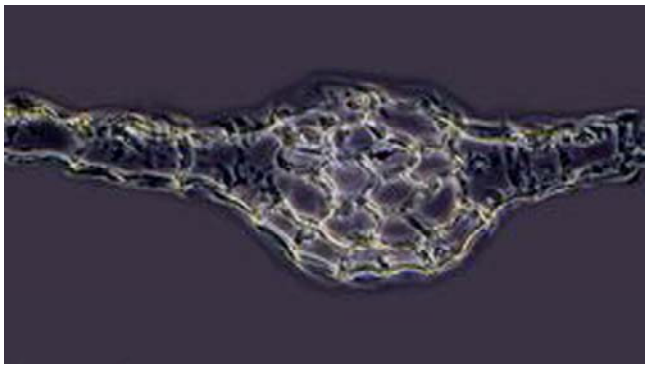

Figure 10. ***Metzgeria furcata*** thallus cross section at midrib. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Ectohydric mosses typically maintain a constant internal water content by absorbing water from the external capillary spaces as needed (Proctor 2000b). The ectohydric and endohydric modes each require their own structural adaptations. Lacking lignin, xylem is not

possible. Furthermore, in the lignified vascular plants, it is the sporophyte generation that carries out organized internal conduction, and the gametophyte, with rare exception, does not. By contrast, in bryophytes it is the leafy gametophyte that must obtain and conduct water and nutrients about the plant, although conduction also occurs in the moss sporophyte (Ligrone *et al*. 2000; see Chapter 5-9).

Although the hornworts (**Anthocerotophyta**) have been considered by some to be reduced from more advanced plants, water-conducting tissue is unknown in this phylum (Ligrone *et al.* 2000), although Hébant (1977) reported the presence of cells resembling phloem sieve cells (leptoids?) in ***Dendroceros*** (Figure 11). Likewise, few liverworts (**Marchantiophyta**) have specialized conducting tissues in their gametophytes (Figure 12-Figure 18), and none have them in the sporophyte. Nonetheless, conducting strands have been known since 1901 in the thallose liverwort ***Pallavicinia lyellii*** (Figure 19; Tansley & Chick 1901). As in mosses, ***Pallavicinia*** conducting strands (Figure 20) closely resemble tracheids, with long cells, tapering ends, and obliquely oriented pits, and they, like xylem cells, are dead at maturity (Richardson 1981).

Figure 11. ***Dendroceros borbonensis***, a hornwort (**Anthocerotophyta**). Photo by Jan-Peter Frahm, with permission.

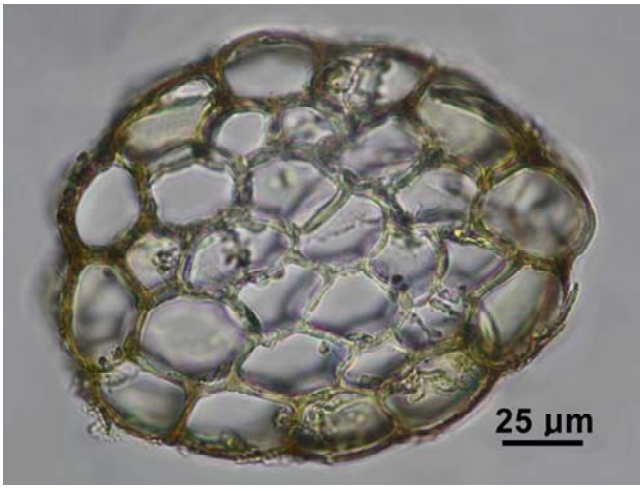

Figure 12. ***Kurzia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

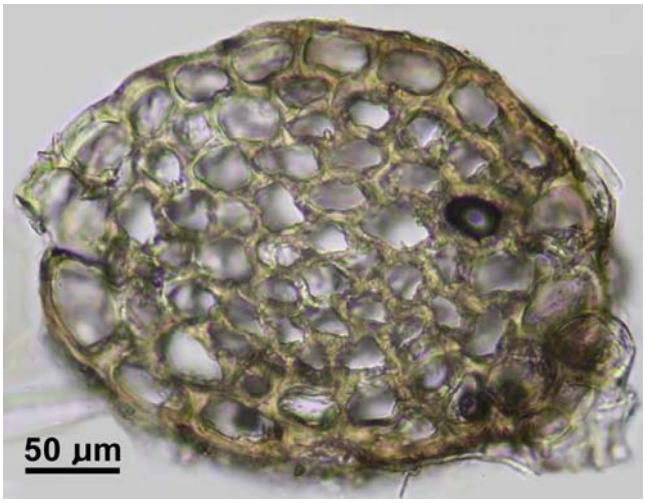

Figure 13. ***Lepidozia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

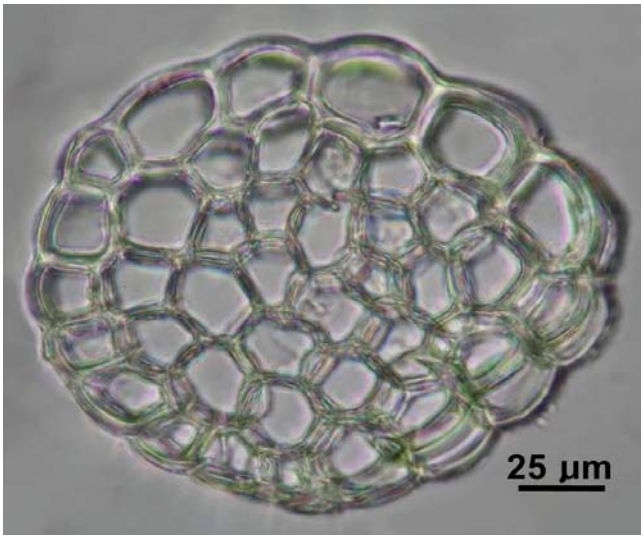

Figure 14. ***Telaranea pallescens***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

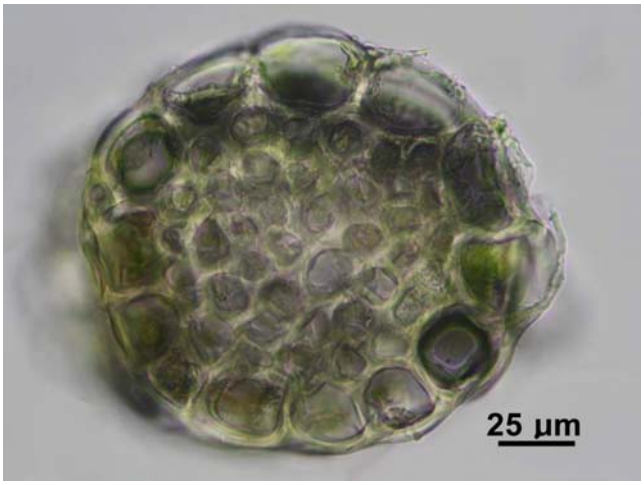

Figure 15. ***Telaranea tridactylis***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

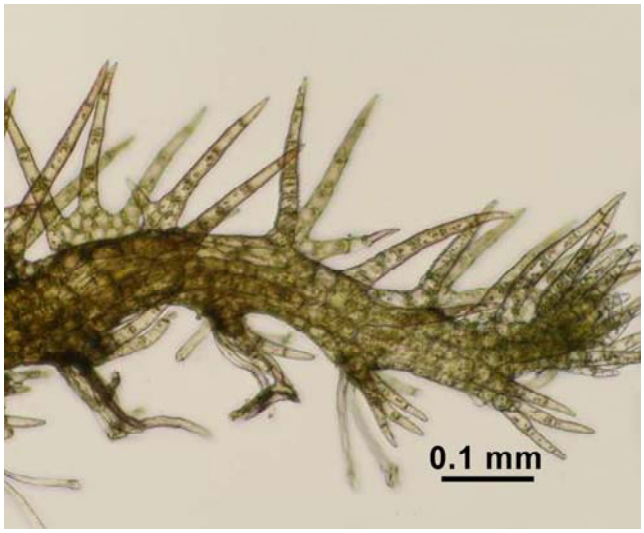

Figure 16. ***Temnoma palmata***, a leafy liverwort (**Pseudolepicoleaceae**, **Jungermanniopsida**). Photo by Tom Thekathyil, with permission.

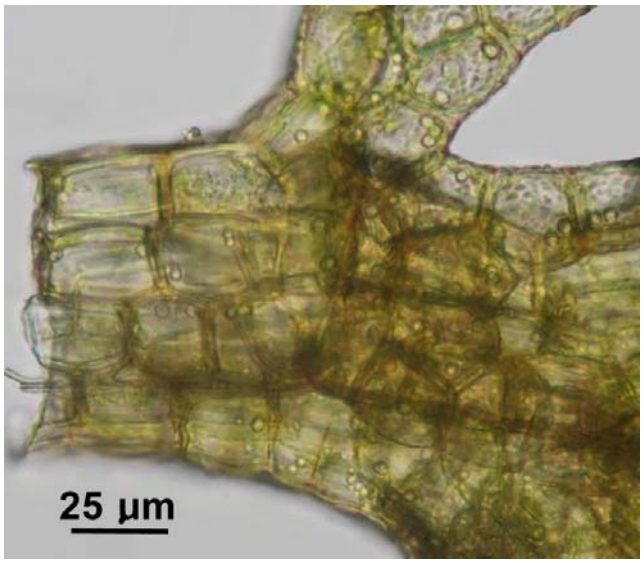

Figure 17. ***Temnoma palmata*** stem showing parenchyma cells and leaf base. Photo by Tom Thekathyil, with permission.

Figure 18. ***Temnoma palmata*** stem cross section. Photo by Tom Thekathyil, with permission.

Figure 19. ***Pallavicinia lyellii*** thallus. Photo by Jan-Peter Frahm, with permission.

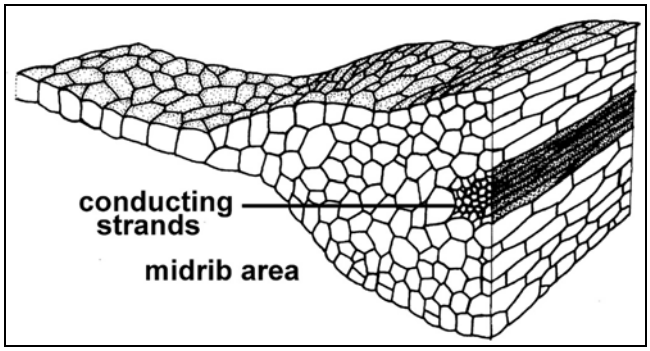

Figure 20. ***Pallavicinia lyellii*** cross section of thallus. Drawing from Hébant (1977).

Unlike the liverworts, as already noted mosses can have conducting cells in both generations (Ligrone *et al.* 2000). In some liverworts of **Calobryales** and in **Pallaviciniaceae** of the **Metzgeriales** (Figure 19-Figure 20) and the moss ***Takakia*** (a primitive moss once thought to be a liverwort; Figure 22), there exist water-conducting cells with perforated walls derived from **plasmodesmatal pores** (Ligrone *et al*. 2000), but these do not seem to be organized into a distinctive **central strand** (group of elongate cells forming central axis of stems and thalli of some bryophytes, usually thin-walled and often colored; Figure 54). Furthermore, the water conducting cells of ***Takakia*** (Figure 21-Figure 23) do not seem to be homologous with either the hydroids of other mosses or with those of the **Metzgeriales** or the leafy liverwort ***Haplomitrium*** (Figure 24), lending support to its basal lineage (Ligrone *et al*. 2000).

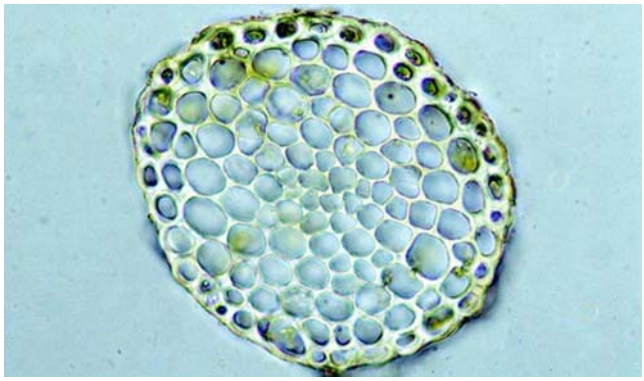

Figure 21. ***Takakia lepidozioides*** stem cross section. Photo from the Herbarium of Hiroshima University, with permission.

Figure 22. ***Takakia lepidozioides*** showing rhizomes and stems. Photo from the Herbarium of Hiroshima University, with permission.

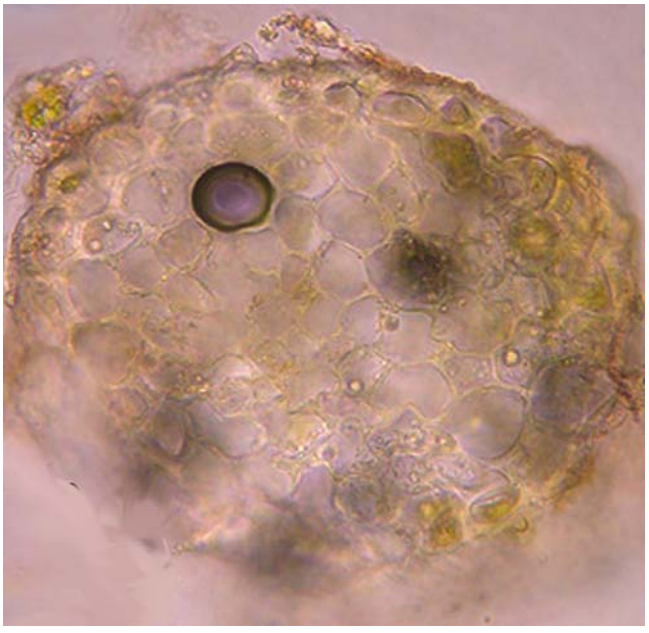

Figure 23. Cross section of stem of ***Takakia lepidozioides*** showing no evidence of a central strand. Photo with permission from Botany website, UBC.

Figure 24. ***Haplomitrium gibbsiae*** showing stems that lack a central strand. Photo by Jan-Peter Frahm, with permission.

Dendroligotrichum dendroides (Figure 25, Figure 45, Figure 69) can reach 60 cm height and transports water **endohydrically** (internally) (Atala & Alfaro 2012). Its water-conducting **hydrome** follows Murray's law, *i.e.* the sum of the radii of the conduits to the third power (Σr^3) is maintained across branching of these conduits. This means that the conduction system is optimized for maximal water transport per unit of 'vascular' tissue biomass. As the vascular tissue ascends toward the apex, there is **acropetal** (base to apex) tapering and an increase in conduit number at ascending levels. Since this architecture is similar to that of tracheophytes, Atala and Alfaro reasoned that it had undergone the same selection pressures in its evolution.

Figure 25. ***Dendroligotrichum dendroides***, a moss with non-lignified vascular tissue. Photo by Felipe Osorio-Zúñiga, with permission.

Leptomes and Hydromes

Kawai (1991a) describes the moss stem as having a basic structure much like that of tracheophytes with an **epidermis** surrounding the **cortex** (Figure 26-Figure 27). This basic structure describes most of the **pleurocarpous** mosses that move internal substances mostly horizontally.

Among the **acrocarpous** mosses (those mostly upright mosses with the sporophyte at the stem apex), more complex stems can have a conducting cylinder in the center of the stem. This cylinder connects the base of the stem to the apex, but in most cases it is not connected to the leaves by any sort of leaf trace. The center of this conducting cylinder is comprised of **hydroids** and **stereids**, making up the **central strand** (Figure 28) (Zamski & Trachtenberg 1976). As you can guess from

the name, **hydroids** are water-conducting cells. They are somewhat similar to tracheids but lack any horizontal connections (*i.e.* no pits) and are not lignified. And as you will see later, their chemistry and development are different from that of tracheids. Hydroids collectively make up the **hydrome** (also known as **hadram** or **hydrom)** (Scheirer 1980).

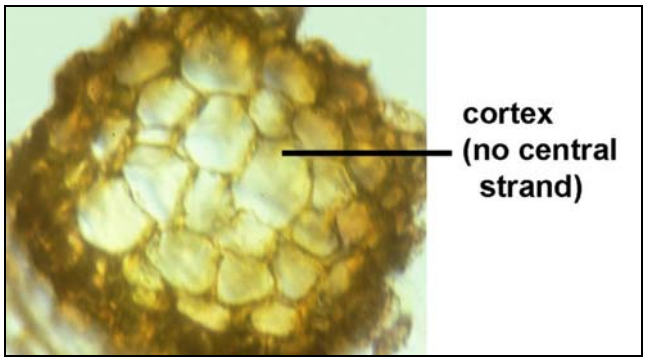

Figure 26. ***Trichodon cylindricus*** stem cs showing lack of central strand. Photo by Janice Glime.

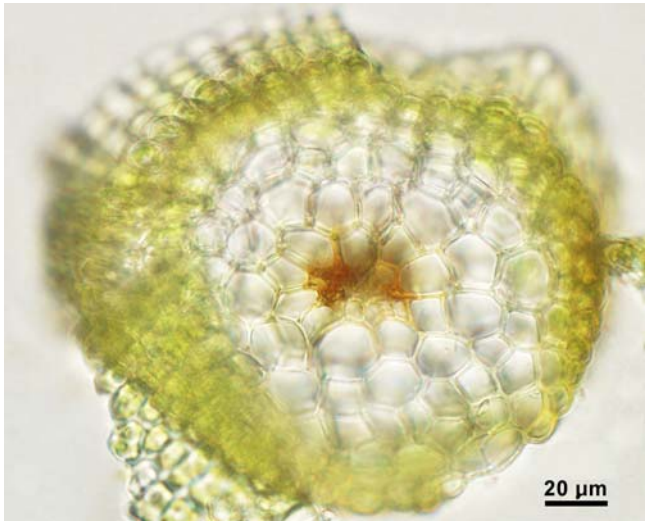

Figure 27. ***Molendoa sendtneriana*** (acrocarpous; **Pottiaceae**) stem cross section showing a central tissue that is differentiated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stereids are elongate, thick-walled, slender, and fiber-like cells that add support to the stem, typically arranged in a cylinder around the hydrome. The stereids are collectively known as the **sterome** (Hébant 1977) (also known as sterom; Zamski & Trachtenberg 1976). They can also occur in the leaf **costa** (midrib-like strand; Figure 57), as will be discussed below, where they also serve as support.

Hébant (1977) describes the living parenchyma cells around the central strand in the **Polytrichaceae** to be a **hydrom sheath**, a term originated by Tansley and Chick (1901). This seems like an unnecessary term with only limited usage. However, Hébant reports that both starch grains and oil droplets are frequent in these cells. In ***Polytrichum commune*** (Figure 3), these cells have accelerated enzyme activity at the same time the protoplasts of the hydroids degenerate. Furthermore, some members of the **Polytrichaceae** have stereids among the central strand cells. These have acid phosphatase activity in ***Dawsonia longifolia*** (Figure 2), suggesting they may have a role in the maturation of the hydroids.

Whereas the hydrome is relatively common, the **leptome** (also known as leptom; Figure 28) is less well known. The simple structure of its cells (**leptoids**) makes them difficult to distinguish from cortex parenchyma cells in cross section, but in vertical section they can be seen as longer cells surrounding the central strand and somewhat resembling phloem sieve cells (Figure 1, Figure 52). Their function, like that of phloem cells, is for photosynthate conduction, but they may also transport hormones or other substances. These cells in the **Polytrichales** (Figure 31) have oblique sieve plates, organized marginal endoplasmic reticulum, and partial nuclear degeneration (Scheirer 1975; Crandall-Stotler 1980).

In mosses like the **Mniaceae** (Figure 28-Figure 30) and **Polytrichaceae** (Figure 31), distinguishing the hydroids is fairly easy. However, not all distinctive cells in the center of the stem are hydroids. In other mosses, small to large cells comprise a distinctive central tissue (Figure 27), but we have no experiments to demonstrate their functions in conduction. It was not until 2002 (Ligrone *et al.* 2002) that immunocytological testing revealed the nature of the central tissue cell walls of 8 mosses and 4 liverworts. Little follow-up work has occurred, hence much of our understanding is still conjecture.

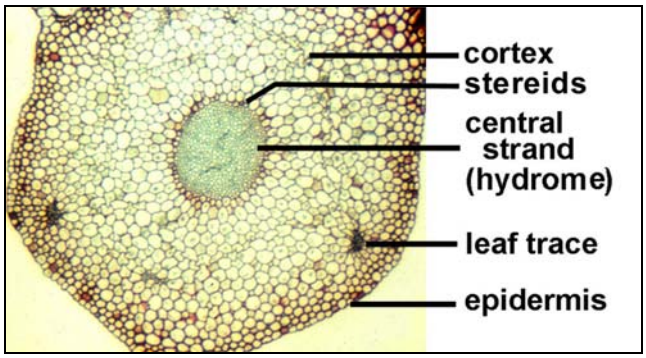

Figure 28. ***Plagiomnium*** (**Mniaceae)** stem cross section illustrating well-developed central strand. Photo by Janice Glime.

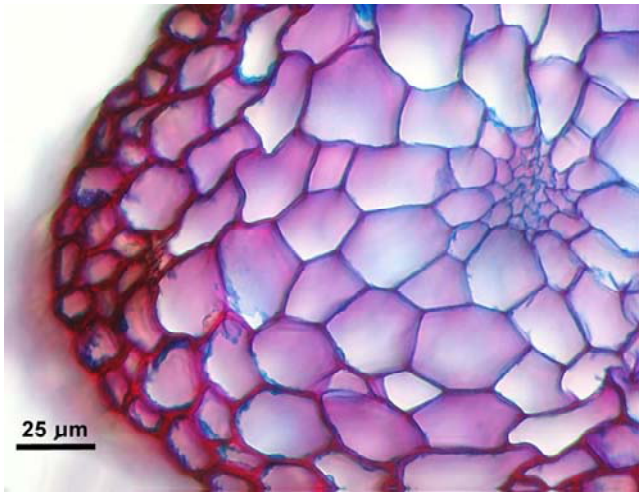

Figure 29. ***Plagiomnium ellipticum*** stem cross section showing central strand with **hydroids**. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

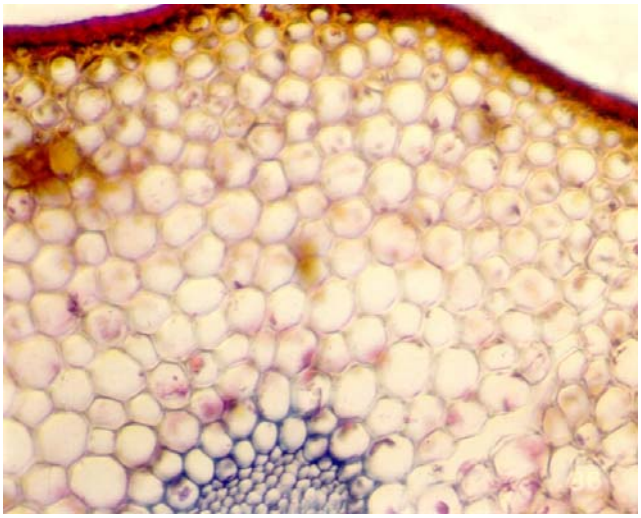

Figure 30. ***Rhizogonium*** (**Mniaceae**) stem cross section showing **hydroids** (stained blue in center). Photo courtesy of Isawo Kawai.

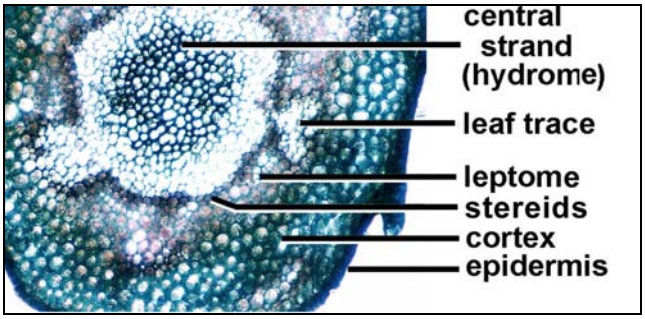

Figure 31. ***Polytrichum*** stem cross section illustrating well-developed central strand. Photo courtesy of Isawo Kawai.

Consider, for example, the genus ***Sphagnum*** (Figure 32). Central cells can vary considerably among species (Figure 33-Figure 38) and can be much smaller than the outer layer that comprises the epidermis (Figure 39). Yet these small cells of the central core are not conducting cells (Hébant 1977). Instead, ***Sphagnum*** typically uses its descending branches as wicks because they form capillary spaces around the stem (Figure 32).

Figure 32. ***Sphagnum obtusum*** showing descending branches that help to create capillary spaces and the wicking activity for upward movement of water. Photo by Michael Luth, with permission.

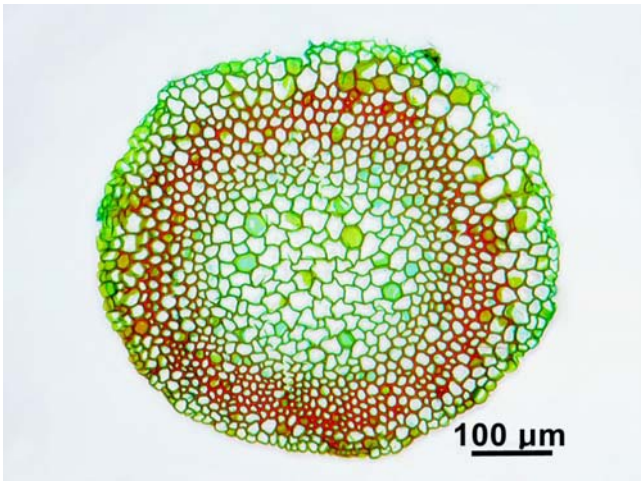

Figure 33. ***Sphagnum obtusum*** stem cross section with larger parenchyma cells in the center, surrounded by smaller thick-walled cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

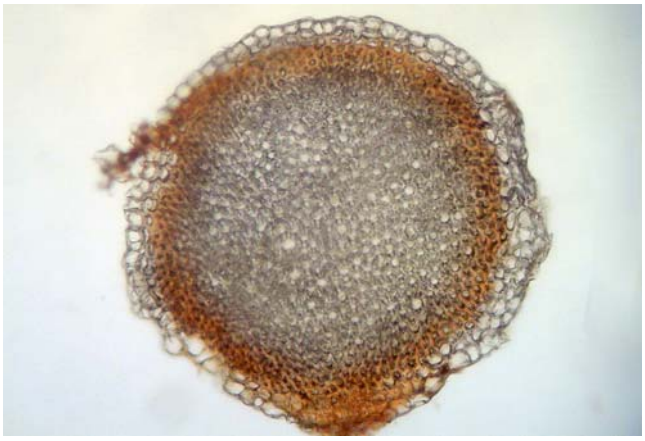

Figure 34. Stem cross section of ***Sphagnum contortum*** with three distinct cell types but no hydroids. Photo by Michael Lüth, with permission.

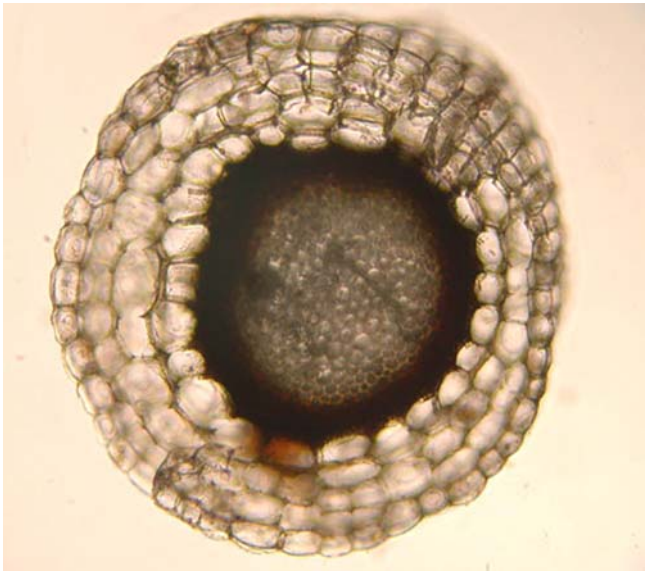

Figure 35. ***Sphagnum*** stem cross section with small-celled central core, dark band of cells, and 3-4 layers of outer hyaline cells. Photo from Botany website, University of British Columbia, Canada, with permission.

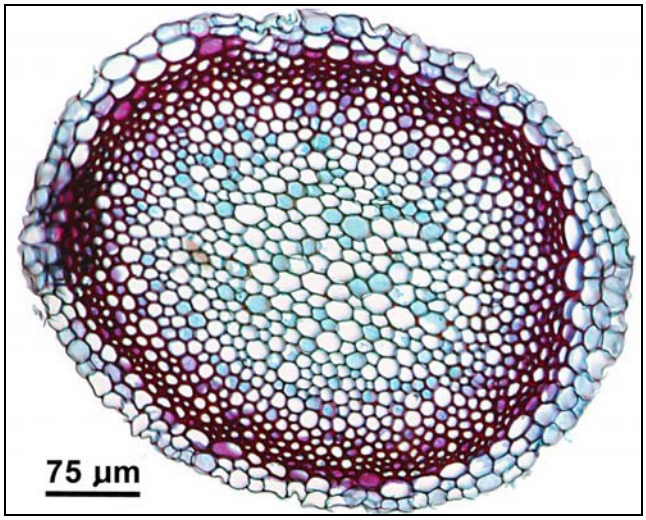

Figure 36. ***Sphagnum squarrosum*** stem cross section with central parenchyma cells, a strengthening layer, and two distinct layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

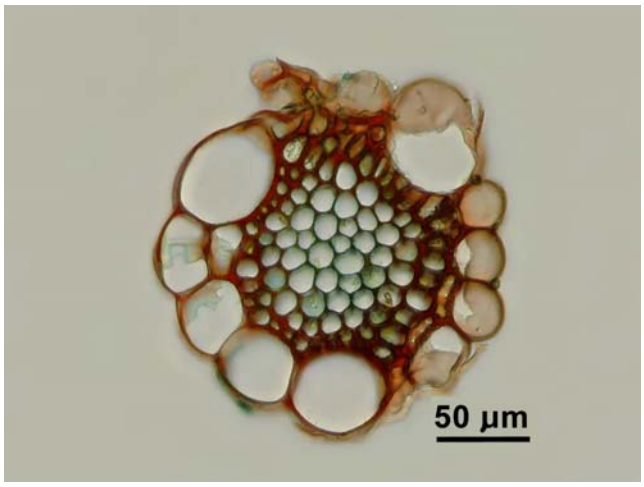

Figure 37. ***Sphagnum squarrosum*** branch cross section showing very different outer hyaline cells and overall appearance from that of the stem in Figure 36. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

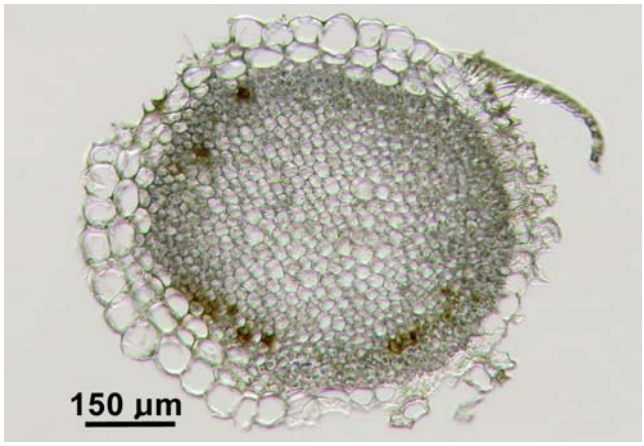

Figure 38. ***Sphagnum fimbriatum*** stem cross section showing only two kinds of cells: central core and outer hyaline cells (**hyalodermis**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

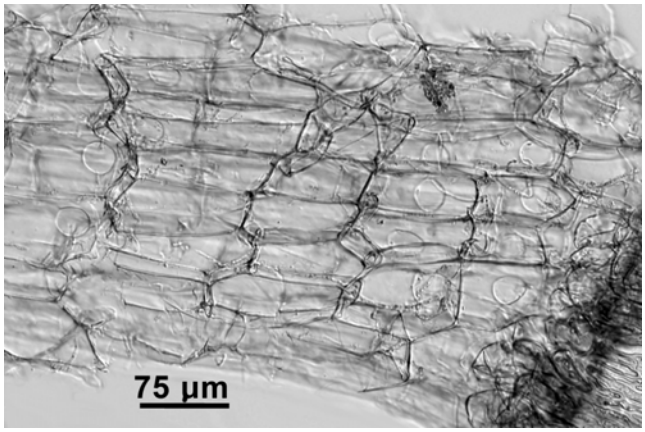

Figure 39. Longitudinal view of ***Sphagnum fimbriatum*** stem hyalodermis showing pores. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Schimper (1857) determined that the hyaline outer cells of stems and the hyaline cells of leaves in ***Sphagnum*** were dead at maturity (Figure 40). Furthermore, they have true perforations strengthened by spiral fibers (Figure 41). Branches are smaller than the stem and typically have a single outer hyaline layer and smaller, often thick-walled cells in the central core (Figure 42-Figure 43).

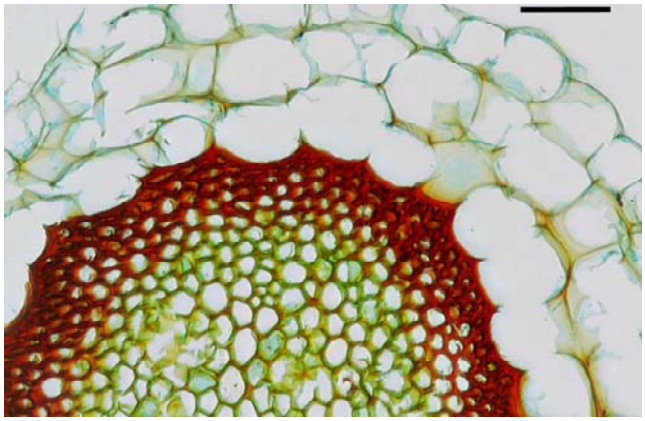

Figure 40. ***Sphagnum papillosum*** stem cross section with central core and dead outer layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

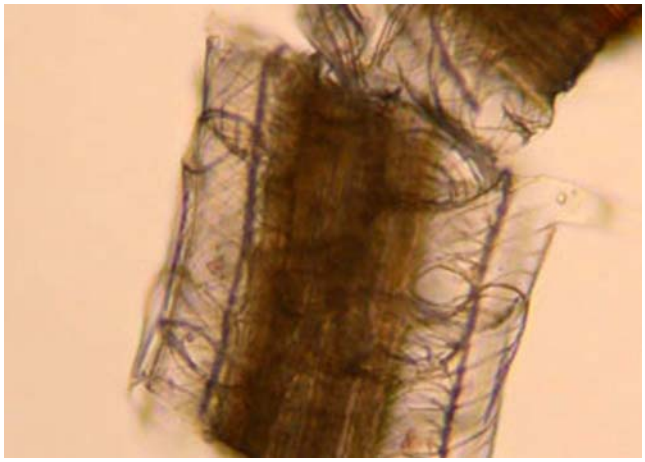

Figure 41. Longitudinal view of ***Sphagnum papillosum*** stem showing **central core** and outer hyaline cells (**hyalocysts**) with **fibrils** and **pores**. Photo from Botany website, University of British Columbia, Canada, with permission.

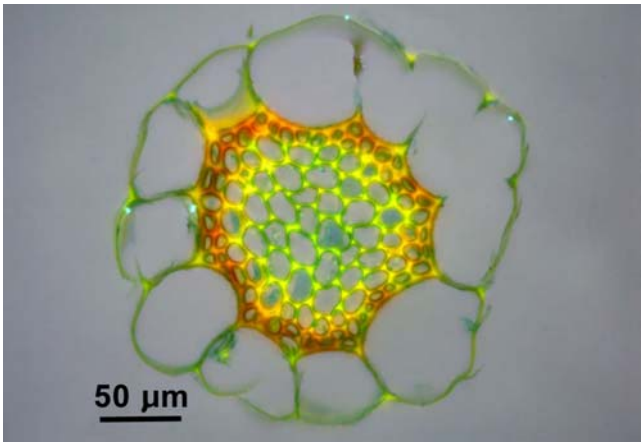

Figure 42. ***Sphagnum papillosum*** branch cross section demonstrating its differences from the stem in Figure 40. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

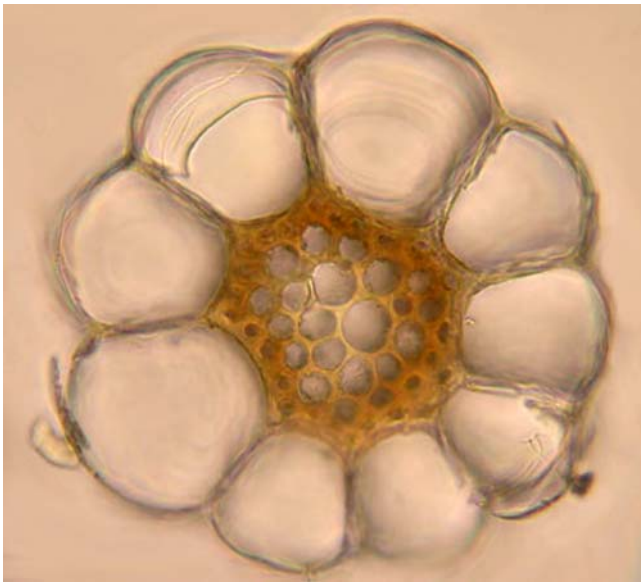

Figure 43. ***Sphagnum papillosum*** branch cross section. Photo from Botany website, University of British Columbia, Canada, with permission.

Schnepf (1973) later found that microtubules are fundamental in the development of the spiral thickenings of ***Sphagnum*** by lifting the plasmalemma off the wall to form an extraplasmatic space in which wall material is accumulated. The wall area where the pore will form becomes progressively thinner until only the cuticle remains. The cuticle eventually ruptures, making a pore. The protoplasts likewise eventually disappear.

The **Marchantiophyta** lack water-conducting cells except for two families of leafy and two of thallose liverworts (Ligrone *et al*. 2000, 2002). These conducting cells are formed by protoplasmic degeneration due to acid phosphatases, as in the mosses, but their wall development is different from that of the mosses (Crandall-Stotler 1980). They lack wall hydrolysis but possess numerous plasmodesmata-derived pores on all walls and never develop polyphenolic compounds (Hébant 1978). No food-conducting cells are known among the **Marchantiophyta** (Figure 44).

Figure 44. ***Porella navicularis*** (**Marchantiophyta**, **Jungermanniopsida** – a leafy liverwort) stem cross section showing absence of central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

Hydroids

The elongated, water-conducting **hydroids** typically occur in groups of 2-3 in bryophyte stems (Hébant 1970); they are similar to tracheids, but lack lignin and secondary wall thickenings (Taylor 1988). Consequently, hydroids are usually thin-walled (Zamski & Trachtenberg 1976) and lack the helices and other thickenings typical of tracheids. Vanderpoorten and Goffinet (2009) sum up three major differences between hydroids of bryophytes and the tracheids and vessels of tracheophytes: hydroids lack secondary wall patterns; bryophyte lignin-like polymers are not cell-specific as they are in tracheophytes and are more likely to offer protection against microbes; hydroids collapse during water stress, making them highly resistant to cavitation (drop in vascular pressure due to vapor pockets resulting from desiccation) (Ligrone *et al.* 2000). This combination creates a fundamental difference in response to drying, with bryophytes being desiccation tolerant and tracheophytes preventing desiccation by pumping water from the soil, closing stomata, and reducing water loss with a waxy cuticle (Vanderpoorten & Goffinet 2009).

Table 1. Comparison of percentage of structural components of tree leaves and of plants of the moss ***Polytrichastrum*** (=*Polytrichum*) ***ohioense***. From Lawrey 1977.

Litter type	soluble carb	hemi-cellulose	cellulose	"lignin"	ash
Pinus resinosa leaves	35.41	13.44	19.37	23.56	3.68
angiosperm tree leaves	43.89	11.59	20.43	11.04	6.97
Polytrichastrum ohioense	16.51	14.07	24.37	12.90*	4.24

*Not a true lignin in mosses.

Hydroids senesce at maturity and become dead, empty cells, like those of xylem, with slanted end walls that abut on the end wall of the next cell, as in tracheids (Richardson 1981). This change from living cells to empty dead cells is a result of acid phosphatase activity that degenerates the protoplasm (Crandall-Stotler 1980). Hydroids of **Bryophyta** typically lack perforations but sometimes have secondary polyphenolic thickenings on the lateral walls of

cells (Scheirer 1975). Scheirer (1973) used ***Dendroligotrichum*** (Figure 45) (**Polytrichopsida**) to demonstrate that hydrolysis leaves behind only cellulose remains of the primary walls of end walls of hydroids. Subsequent examination by electron-dense crystals of Prussian blue on the end walls in ***Polytrichum commune*** (Figure 46) suggests that these end walls are highly permeable (see Figure 47), but that substances are unable to move through the lateral walls (Scheirer & Goldklang 1977).

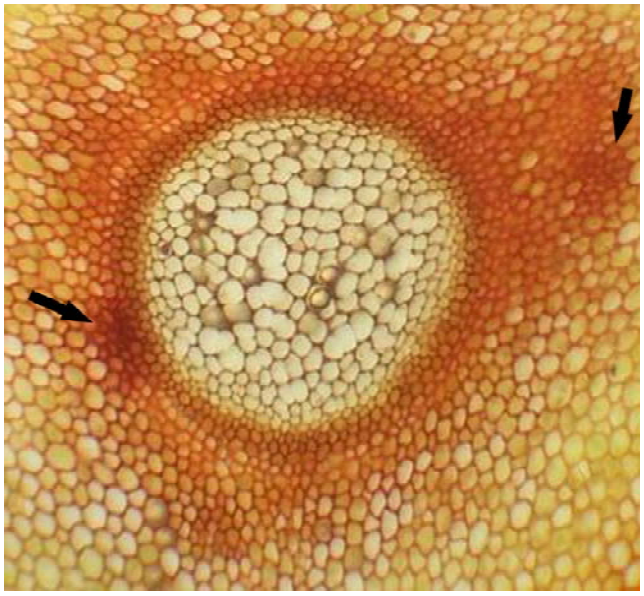

Figure 45. ***Dendroligotrichum dendroides*** stem cross section showing hydroids in center (**brown walls and mostly empty**), surrounded by stereids (**brown walls and interior brown**) and leptoids (**rusty-colored walls and contents**). Note vascular branches (**arrows**) that go into the cortex. The central strand has a few sclereids (thick walls) and these are living cells. Photo by Juan Larrain, with permission.

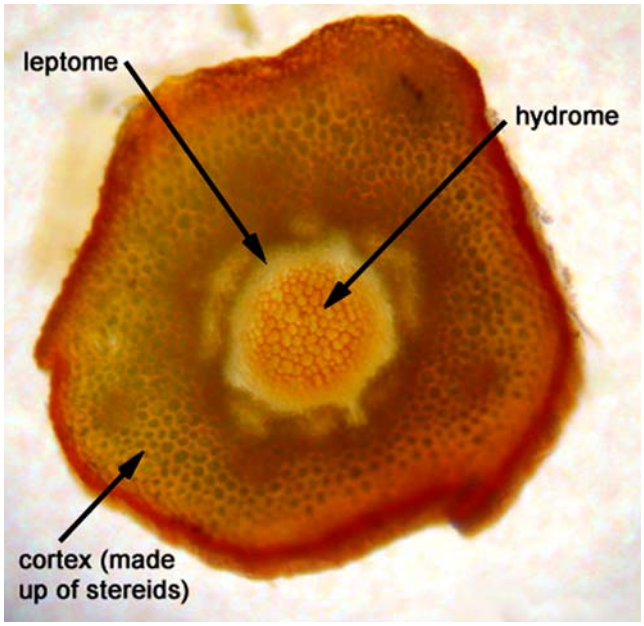

Figure 46. ***Polytrichum commune*** stem cross section. Photo by Julie Chou from Botany website, University of British Columbia, Canada, with permission.

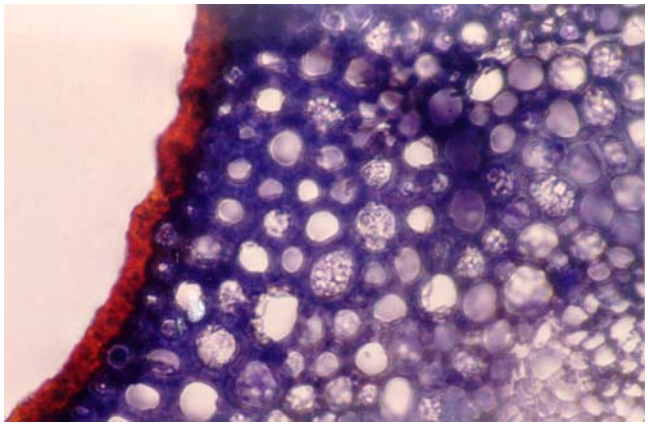

Figure 47. Cross section of ***Polytrichum*** stem stained with aniline blue to show thin areas in end walls of cortical cells. Photo courtesy of Isawo Kawai.

To understand any relationship between hydroids of bryophytes and tracheids or vessels of tracheophytes, we must understand their structure. We can consider that part of their structural development is similar to that of tracheophytes because they, like xylem cells, are dead at maturity (Richardson 1981). But is their chemical nature similar? It appears that the bryophytes have derived their water conducting cells in a variety of ways.

Hébant (1973a) found that strong activity of acid phosphomonoesterases occurs in the differentiating water-conducting cells of various mosses and at least one liverwort. But a lesser activity is also present in leptome cells and certain parenchyma cells of some **Polytrichales**.

Some chemical labelling tests gave similar results in as divergent taxa as ***Takakia*** (Figure 21-Figure 23) and ***Polytrichum*** (Figure 46-Figure 47), but different results in ***Mnium*** (Figure 70) (Ligrone *et al*. 2002). And Ligrone and coworkers found labelling of both water-conducting cells and parenchyma cells in ***Haplomitrium*** (Figure 98), but only of water-conducting cells in ***Polytrichum***. Ligrone *et al*. found that the arabinogalactan protein (AGP) antibody labelled the water-conducting cells in all Bryophyta tested (8 species) except the large polytrichaceous moss ***Dawsonia*** (Figure 48). No labelling occurred in the liverworts (4 species). Hence, it appears that the chemicals present are similar, but that they occur at different places within the plants.

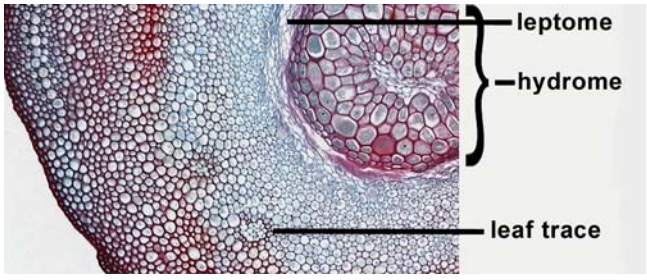

Figure 48. ***Dawsonia*** stem cross section to show hydrome, leptome, and leaf traces. Photo from Wikimedia Creative Commons.

Differences in labelling between the water-conducting cells and the cortical cells appeared to be mostly quantitative in these few species (Ligrone *et al*. 2002). On

the other hand, electron microscopy revealed clearly distinct differences in the location of the antibodies within the cell walls of these two cell types, suggesting that their presence in a particular location was tissue specific in its regulation. Even within the **Polytrichaceae** (Figure 45-Figure 48) there is considerable diversity in the immunocytochemistry. In short, the bryophytes have a widely diverse chemistry in their conducting cells, but as such, they differ strongly from those of tracheophytes. Ligrone *et al*. (2002) consider the presence of several carbohydrate antigens in the cell walls of hydroids to indicate that hydrolysis of non-cellulosic polysaccharides is not part of the maturation process, a strong contrast to that in tracheophytes (see Hébant 1977).

Accompanying these chemical differences are differences in structure. True **perforation plates** (end walls of vessels) have not been found in **Polytrichaceae** (Figure 45-Figure 48) (Frey & Richter 1982) or most other mosses (Hébant 1973b). Consequently, Frey and Richter (1982) set out to discover them in mosses. In the dendroid moss ***Canalohypopterygium tamariscinum*** (Figure 49), they found structures resembling perforation plates of *Ephedra* (Gnetophyta), although they were not numerous and were restricted in location to branching areas. Perhaps this type of vascular structure permits them to be dendroid, lacking the close structure of leaves along the stem needed for capillary action. Smith (1964) had already demonstrated perforations in the conducting elements of the liverwort ***Symphyogyna circinata*** (Figure 50). Furthermore, pits are known, particularly in end walls, from ***Haplomitrium*** (Figure 98) [considered to be basal to leafy liverworts (Crandall-Stotler & Stotler 2000)] and ***Takakia*** (Figure 21-Figure 23) (now classified as a primitive moss in the **Takakiopsida**), as confirmed by electron microscope.

Figure 49. ***Canalohypopterygium tamariscinum***. Photo by Pieter Pelser, with online permission for educational use.

Although hydroids do not seem to contain true lignin, as do tracheophyte xylem cells, they do contain a polyphenolic cell wall component that functions similarly to lignin (Pressel *et al*. 2010). This compound protects the wall from hydrolytic attack and aids in internal transport of water. In ***Rhacocarpus purpurascens*** (Figure 51), Edelman *et al*. (1998) found walls composed of "mainly lignin, **hemicellulose** (H-bonded to cellulose in plant cell walls), and cellulose in a ratio of ca. 9:8:5." Although the resonance spectrum indicated various characteristics typical of lignin, some specific peaks associated with known lignin compounds were missing. Thus the question remains, is this true lignin?

Figure 50. ***Symphyogyna circinata***. Photo by Filipe Osorio, with permission.

Figure 51. ***Rhacocarpus purpurascens***, a moss that produces a cell wall substance similar to lignin. Photo by Michael Lüth, with permission.

Leptoids

Leptoids (Figure 52) are very similar to phloem sieve cells, and in fact, Behnke (1975) calls them just that. Taylor (1988) considers that in some cases they are nearly identical to protophloem cells of certain tracheophytes. They, along with parenchyma cells, comprise the **leptome** (=leptom) (Hébant 1970, 1974; Behnke 1975; Figure 28). We know that they are typical in the **Polytrichaceae**, but have also been found in ***Sphagnum***, **Hookeriaceae**, **Neckeraceae**, and **Orthotrichaceae** (Ligrone & Duckett 1994, 1998; Duckett & Ligrone 2003). Except in the setae of a few species (Hébant 1974), leptoids have not been found in the arthrodontous mosses (considered more advanced) and are unknown in liverworts. It is likely that they are much more common than we realize because in cross section without stain they appear no different from the unspecialized parenchyma cells.

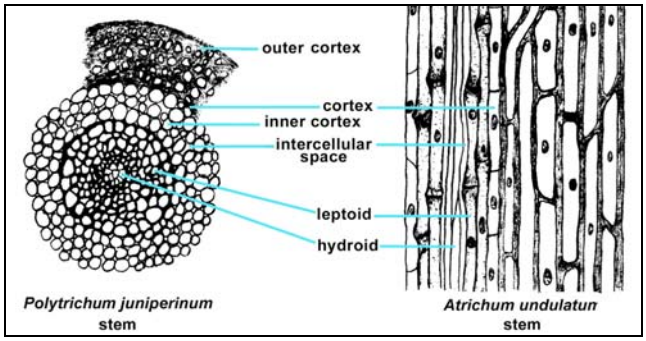

Figure 52. Cross section of ***Polytrichum juniperinum*** and longitudinal section of ***Atrichum undulatum*** stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, modified from Hébant (1977).

In the moss family **Polytrichaceae** (Figure 52, Figure 54), leptoids have an axial system of microtubules with polarized cytoplasmic organization (Ligrone *et al*. 2000). In other mosses, including ***Sphagnum*** (Figure 32-Figure 43), such organization may also occur in stem and seta parenchyma cells. Even rhizoids and caulonemata of mosses and liverworts and thallus parenchyma cells of liverworts may have a similar organization for transporting nutrients **symplastically** (through cells, inside the membrane) for longer distances. But, as will be seen later in this chapter, these food and water conducting cells are fundamentally different from the phloem sieve cells and tracheids of tracheophytes. Nevertheless, Ligrone *et al*. (2002) found that the cell wall and tissue complexity of bryophytes are "on a par with higher plants."

The **leptoids** are distinct in vertical section by their elongate shape and slightly oblique end walls (Figure 55) (Behnke 1975). At maturity, the nucleus degenerates, as in phloem sieve cells (Richardson 1981), but protoplasm remains. In ***Polytrichum*** (Figure 52), the leptoids are not connected end-to-end by sieve plates or pores as in tracheophytes, but by numerous **plasmodesmata**. However, Cortella and coworkers (1994) considered the thin areas of central strand parenchyma cells to be primary pit fields in ***Hookeria lucens*** (Figure 53) stems and suggest that these cells have a conducting function.

Figure 53. ***Hookeria lucens***. Photo by Jiří Kameníček, with permission.

Even the development of leptoids seems similar to that of phloem sieve cells. During leptoid maturation in **Polytrichaceae**, **ribosomes** (centers of protein synthesis) disintegrate and nuclei become smaller and inactive, although they do not dissolve completely as in tracheophytes; mitochondria persist. The parenchyma cells contain starch-storing chloroplasts. As in their tracheophyte counterparts, leptoids move carbohydrates and other substances away from the apex.

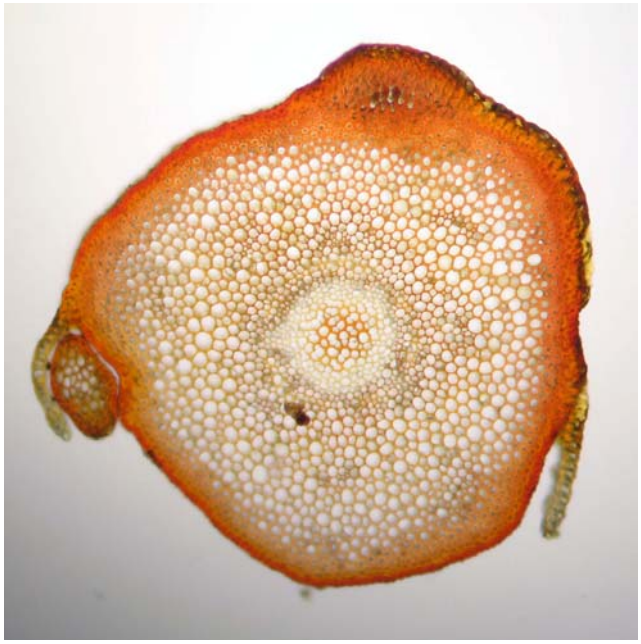

Figure 54. ***Polytrichastrum formosum*** stem cross section showing central **hydroids** (**with orange walls in center**) and considerable differentiation in the cells of the **central strand**. **Leptoids** are present outside the central strand and are not discernible in cross sectional view. Photo from Botany website, University of British Columbia, Canada, with permission.

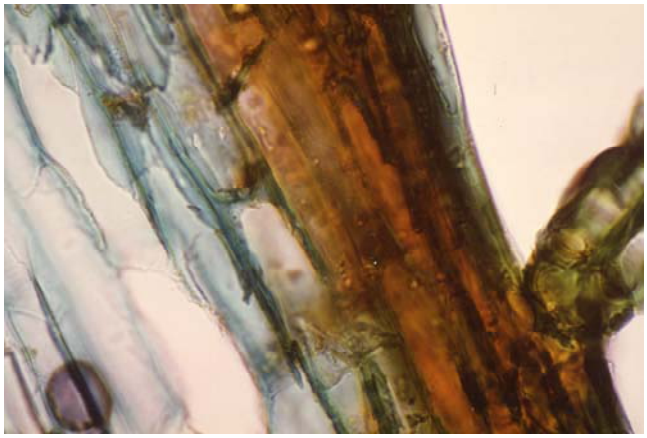

Figure 55. ***Hypnum*** sp., a pleurocarpous moss, stem longitudinal section. Note the long cell with what appear to be broken side walls, a disintegrating diagonal cross wall, and a partially missing protoplast. This appears to be a **leptoid**, but we need conduction tests to verify it. Photo courtesy of Isawo Kawai.

Rhizome

The **rhizome** (underground, horizontal stem connecting upright plants), on the other hand, has

hypodermal and **radial strands** but lacks connecting traces and a sterome. The **hypodermis** (Figure 56), also present in some stems, consists of one to several layers of distinct cells just beneath the epidermis and may be thick-walled or colored.

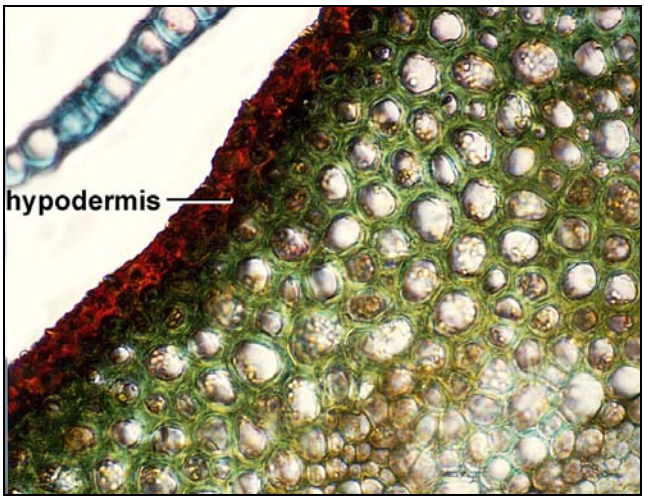

Figure 56. ***Polytrichum*** stem cross section showing **hypodermis**. Photo courtesy of Isawo Kawai.

Long-distance transport brings its own set of problems. These plants can undergo transpiration, causing them to lose water (Raven 2003). In some liverworts and many mosses, but not hornworts, there are dead cells in the tissues. These may function in long-distance **apoplastic** (outside cell membranes) water transport. Symplastic transport, on the other hand, seems to have a high resistance to flow, emphasizing the importance of apoplastic movement.

Leaves

In most tracheophytes, the leaf is a critical structure in creating the movement of water from the roots to the tops of tall plants. This movement, known as the **transpiration stream**, requires the loss of water from the leaf, creating a vapor pressure deficit that brings water upward like someone sucking on a straw. But bryophytes typically do things quite differently, as we shall see in a later sub-chapter. They typically take in water from above, not below, hence requiring a new look at the role of leaves in water movement. It appears that the greatest need is not to move water to the leaves, but rather to move substances made in the leaves to other parts of the plants.

Costa

Within the leaf, water may move cell to cell among the **lamina** cells (Figure 57), but many leaves have a **costa** (Figure 57-Figure 58) that is often accompanied by supporting **stereid** cells (Figure 59). Unlike the midrib of ferns and seed plants, the costa does not branch and rebranch to deliver water or other substances to or from cells of the leaf lamina (Figure 58), although in some taxa, for example ***Hygrohypnum*** (Figure 60), it may have one or more branches. Nevertheless, the costa has elongate cells that we might expect to facilitate a more rapid movement of water within the leaf (Figure 58), but does it?

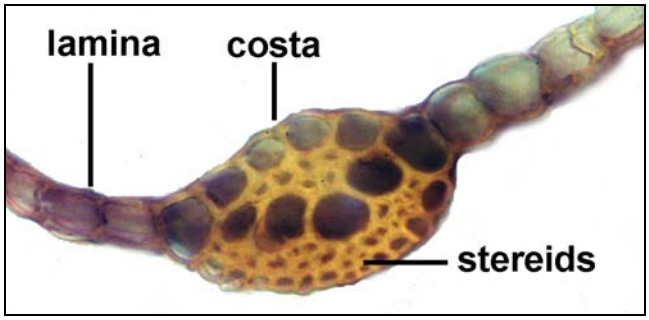

Figure 57. Cross section of moss leaf blade showing arrangement of broad portion (lamina), costa, and supporting stereids. Large cells in costa serve for conduction. Photo by Janice Glime.

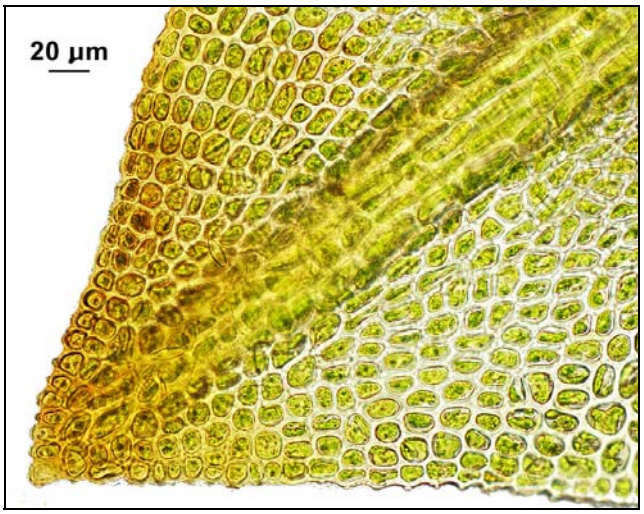

Figure 58. ***Crumia latifolia*** leaf showing elongate costa cells and nearly isodiametric lamina cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

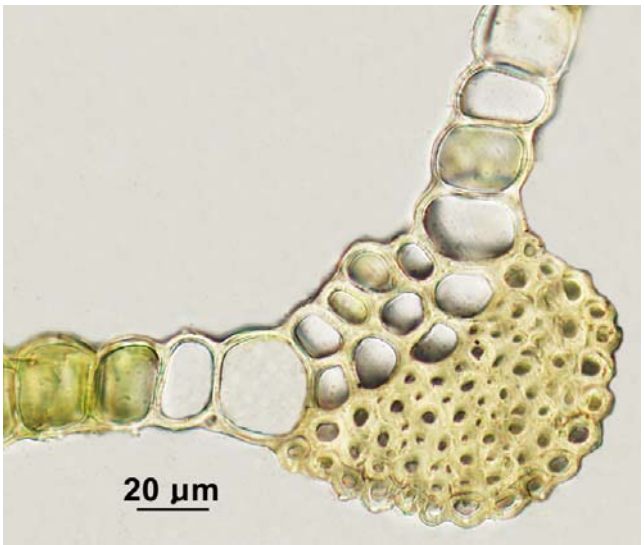

Figure 59. ***Crumia latifolia*** leaf cross section showing enlarged costa with many stereids supporting the conducting cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

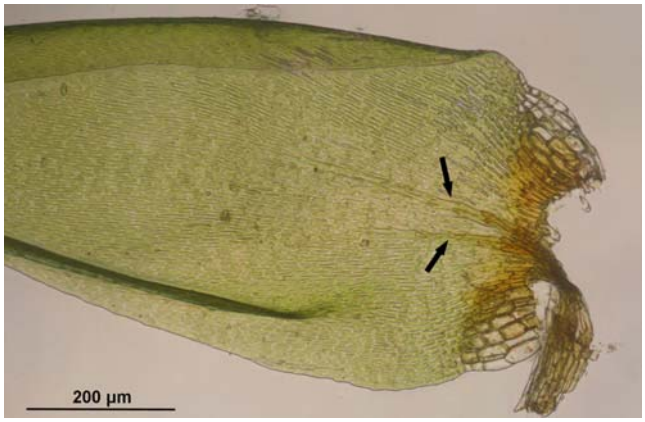

Figure 60. ***Hygrohypnum eugyrium*** leaf showing two branches of the costa (**arrows**). Photo by Hermann Schachner, through creative Commons.

On closer examination of the costa, we find that those elongate cells are living cells with oblique end walls, thin cell walls, and living protoplasm (Hébant 1977)! These are not hydroids, but are **leptoids**. Hence, it appears that in addition to its supporting role, the costa can have the role of conducting substances from the leaf toward the stem. (We will see shortly how this system connects to the leaf traces in the stem.) It appears that the costa should not have a role in conduction of water.

Sphagnum

Sphagnum (Figure 61) has the most unusual water system in its leaves of any bryophyte. Its leaves have two types of cells, and rarely a border in addition. These two types are the water-holding, colorless, dead **hyaline** cells and the green **chlorophyllose** (**photosynthetic**) cells (Figure 62-Figure 63). The hyaline cells serve as water reservoirs for the photosynthetic cells. Their walls have true perforations and are strengthened by spiral thickenings, suggesting the structure of tracheophyte vessels (Figure 62-Figure 63) (Hébant 1977). The pores (perforations) begin with a thinning of an area of the cell wall and presence of a thin membrane. Eventually these rupture to create the pore, using the process already described above for the hyaline cells of ***Sphagnum*** stems.

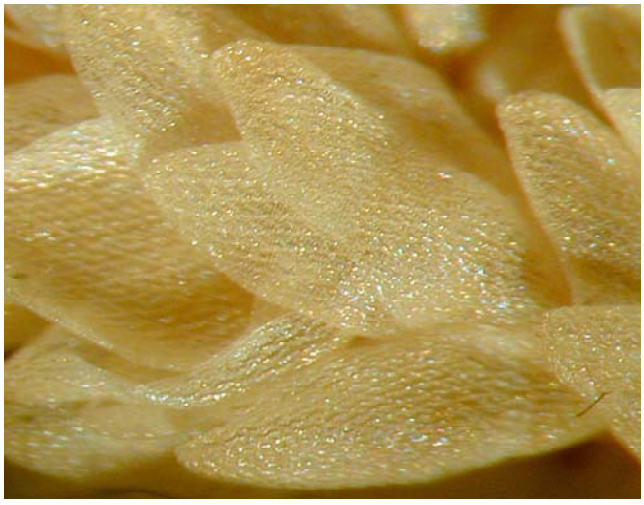

Figure 61. ***Sphagnum*** leaves showing the patterning caused by the network of chlorophyllose cells and hyaline cells. Photo by Michael Lüth, with permission.

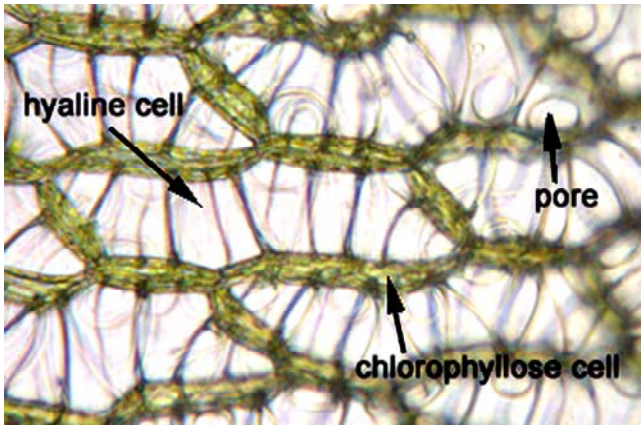

Figure 62. ***Sphagnum*** cells showing hyaline cells with spiral thickenings and pores, intermixed with chlorophyllose cells. Photo from Botany website, University of British Columbia, Canada, with permission.

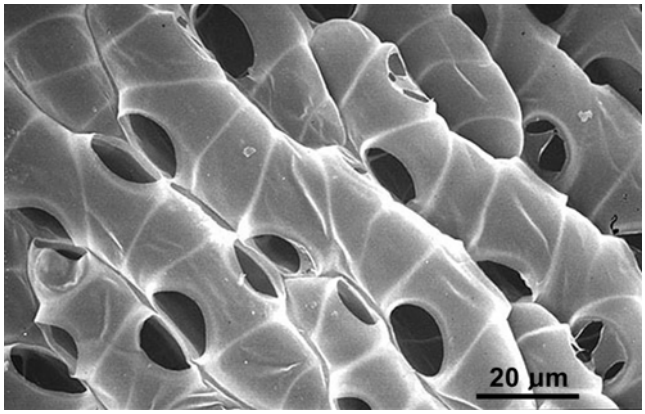

Figure 63. ***Sphagnum*** hyaline cells with spiral fibrils and pores. The photosynthetic cells are hidden by the hyaline cells in this leaf. Photo from Botany website, University of British Columbia, Canada, with permission.

Leafy Liverworts

Leafy liverwort leaves never have a costa (Figure 64), leaving us to assume that transport of water and other substances in the leaves, if needed, is cell-to-cell transport through ordinary leaf parenchyma cells. But in this group (**Jungermanniopsida**), leaves are never more than one cell thick, giving all cells direct exposure to water from the atmosphere or other surroundings.

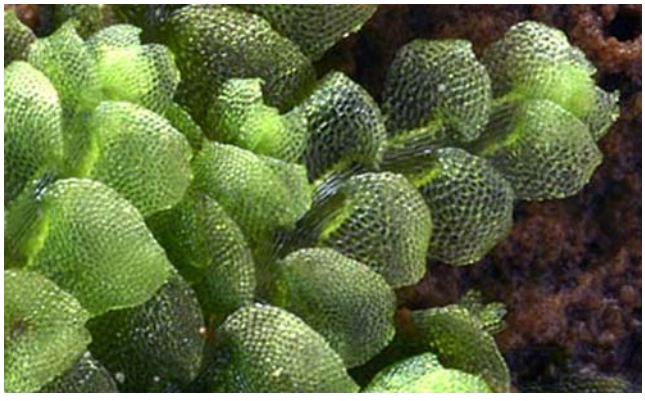

Figure 64. ***Calypogeia fissa*** (**Jungermanniopsida**) showing absence of costa in leaves and one-cell-layer leaf thickness. Photo by Des Callaghan, with permission.

We might also ask the role of **underleaves** (Figure 65) in this group. These may be non-existent (*e.g.* ***Jamesoniella***, Figure 66) to quite large (*e.g.* ***Porella***, Figure 67). Underleaves may be an evolutionary left over with no function, but their persistence suggests they may offer some advantages in water retention. They create capillary spaces on the under side of the stem and thus may aid in water retention. This space may also aid water uptake by holding water, but in many cases this would require that the stem (Figure 68) absorb the water. It would be interesting to experiment with different types of underleaves to see how they affect water uptake, especially by the stem, and how long they are able to hold a water reservoir.

Figure 65. ***Calypogeia integristipula*** demonstration of underleaves. Photo by Michael Lüth, with permission.

Figure 66. ***Jamesoniella undulifolia*** showing absence of underleaves (**arrow**). Photo by David T. Holyoak, with permission.

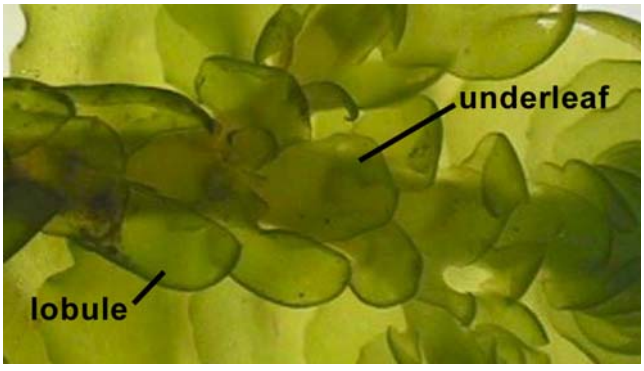

Figure 67. ***Porella platyphylla*** showing its large underleaf and lobule. Photo by Paul Davison, with permission.

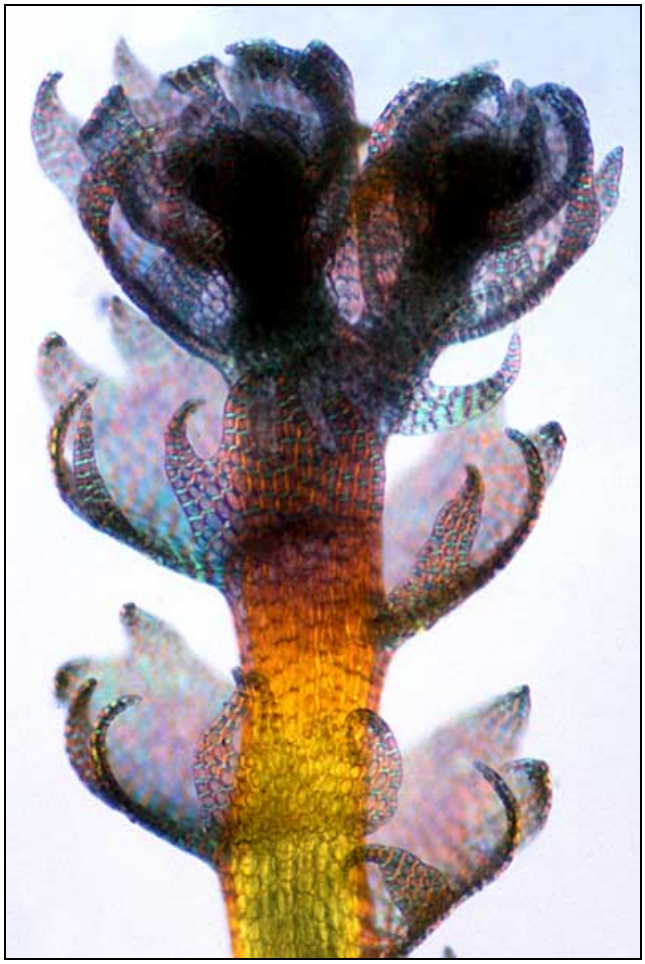

Figure 68. Leafy liverwort showing parenchymatous cells of stem. Photo by Bill Malcolm, with permission.

Another water reservoir in a number of leafy liverworts is the **lobule** (Figure 67). This structure, present in ***Frullania***, ***Porella***, **Lejeuneaceae**, and others can create a small reservoir of water suitable for small aquatic invertebrates such as rotifers and Protozoa to carry out their entire life cycle. These are discussed further in Chapter 7-4.

Leaf Traces

Conduction from stems into leaves is typically through the parenchyma cells of the stem cortex, as will be described in a later sub-chapter. True **leaf traces** (conducting cells connecting the leaf costa to the hydrome; Figure 69) exist in some **Polytrichales**, but in other cases they do not quite reach that far. In the **Mniaceae** and **Splachnaceae** there are **false leaf traces** (Figure 70) that extend into the cortex from the leaf but do not connect with the central strand of the stem (Figure 71) (Hébant 1977). In ***Funaria hygrometrica***, some specimens have true leaf traces that reach the central strand, and others do not.

Hébant (1969) found that in ***Polytrichum*** (Figure 4), the true leaf traces extend from the leaf costa toward the central strand, but they become reduced near the central strand. Nevertheless, Hébant (1969) found that 7-8 hydroids of each leaf trace could connect to the central strand in grassland ***Polytrichum commune*** (Figure 46). This connection, however, seems to be related to water availability. In bog populations, only three hydroids form

the connection. For specimens grown under water, no leaf traces connected to the central strand.

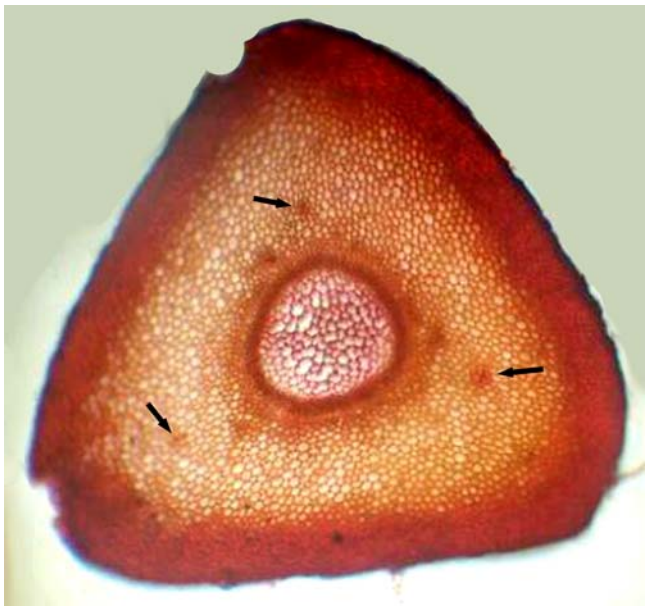

Figure 69. ***Dendroligotrichum dendroides*** stem cross section showing leaf traces in the cortex (**arrows**). Photo by Juan Larrain, with permission.

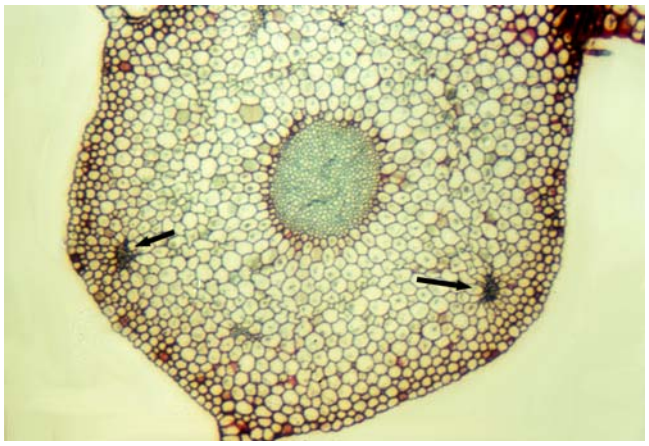

Figure 70. ***Mnium*** stem cross section showing distinct central strand and false leaf traces (**arrow**) that do not connect directly to the leaves. Photo by Janice Glime.

Figure 71. ***Rhizomnium glabrescens*** leaf cross section showing hydroids in center and stereids near the outer margins. In this family (**Mniaceae**), the central strand produces false leaf traces that do not connect to the costa of the leaf. Photo from Botany website, UBC, with permission.

But wait! Many kinds of leaves have a **costa**, the rib that extends part way or all the way down the center of the leaf. But the costa cells are fairly wide cells, albeit elongated, and contain a living protoplast (Hébant 1977). The end walls are oblique and have numerous plasmodesmata. They are in fact **leptoids**, not hydroids, and do not seem to have an important water conducting function in many mosses, if any. Rather, they conduct **photosynthate** and other substances from the leaf to the stem. These materials are thus deposited in the stem tissue. Could these actually connect with leptoids in the stem, permitting transport to stem tips or to rhizomes? In fact, in ***Polytrichum commune*** they do connect to the leptoids of the stem axis. Why then are there hydroids in the leaf traces? What do they connect? Is there any correlation between having a costa with leptoids and a stem with a central strand? Do all leaf leptoids connect with stem leptoids? So little we know...

Sporophyte Conduction

In tracheophytes, it is the sporophyte that has the vascular tissue, and in the setae of mosses, one might find conducting tissues (a central strand) even when it is absent in the gametophyte. This should not be too surprising since the gametophyte is much better adapted to absorbing water from the atmosphere than the cuticle-endowed sporophyte. It is most likely necessary for a number of substances to be transported from the gametophyte into the sporophyte as it develops. And as we might expect, these conducting strands in setae are best developed in the **Polytrichaceae** (Hébant 1977), a family in which the peristome exhibits the more primitive character of nematodontous teeth.

Is perhaps no coincidence that a species with a vascularized stem also has a vascular seta. This seems to be the case in ***Plagiomnium undulatum*** (Figure 72).

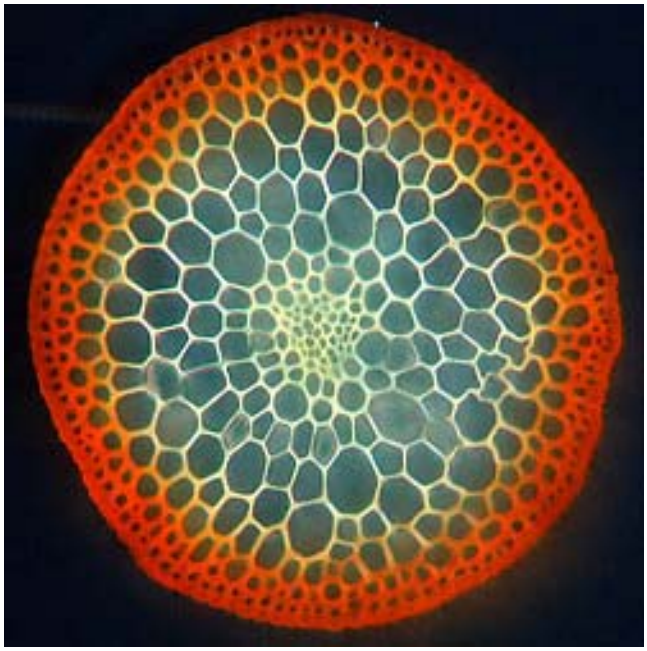

Figure 72. ***Plagiomnium undulatum*** seta cs showing central conducting strand. Photo by Norbert J. Stapper, with permission.

On the other hand, leptoids can occur in the setae of some arthrodontous mosses even when they are absent in the gametophytes. Nevertheless, leptoids of setae, unlike those of tracheophytes, show less differentiation than in their gametophytic counterparts. In the setae of the **Polytrichaceae**, leptoids are not intermixed with specialized parenchyma cells and apparently lack enlarged plasmodesmata in their end walls, as seen in gametophytes of some taxa (Hébant 1974). To add interest to the picture, the leptoids are present in forms that are transitional between the parenchyma cells and the fully differentiated leptoid cells (Hébant 1974).

Meager evidence exists for the presence of **leptoids** in setae of other genera. Among these are ***Funaria***, ***Meesia***, and ***Splachnum*** (Hébant 1977). In ***Tortula muralis*** (Figure 73), Favali and Gianni (1973) have claimed that the leptoids are intermixed with the parenchyma cells in the seta and a similar claim was put forth by Bassi and Favali (1973) for ***Mnium orthorrhynchum***, but Hébant (1977) was unable to find any convincing evidence that this was true in either case.

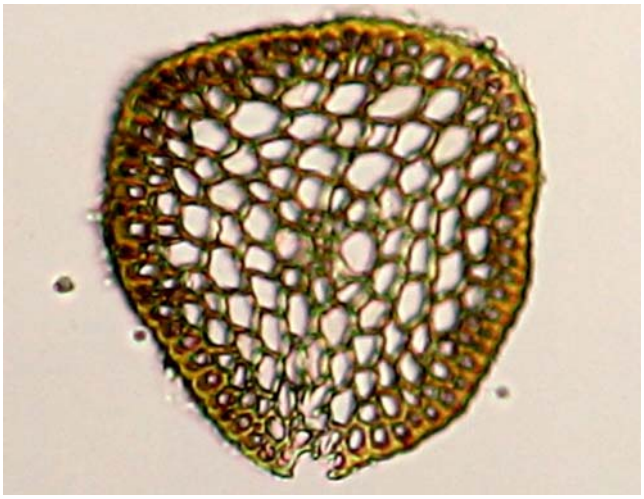

Figure 73. ***Tortula muralis*** seta cross section showing modified cells in center of seta. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 74. ***Tortula muralis*** or ***plinthobia*** stem cs. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stem sections indicate that at least a central strand is present in the acrocarpous mosses ***Dicranum scoparium*** (an **arthrodontous** moss; Figure 75-Figure 76) and ***Tetraphis pellucida*** (a **nematodontous** moss; Figure 77-Figure 78). The presence of leptoids cannot be determined from these views, nor can the function of the central strand. Cross sections of these setae can be compared with stems of the same species in Figure 73-Figure 78.

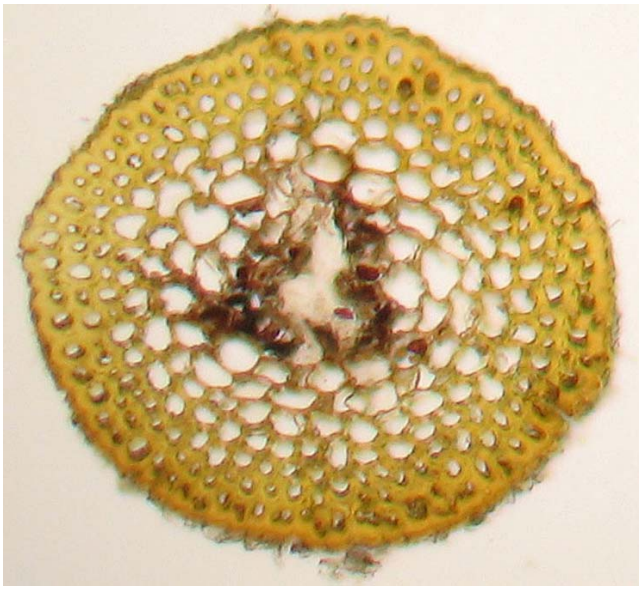

Figure 75. ***Dicranum scoparium*** seta cross section showing broken center with modified cells similar to those of stem (Figure 76). Leptoids do not seem to be visible. Photo from Botany website, UBC, with permission.

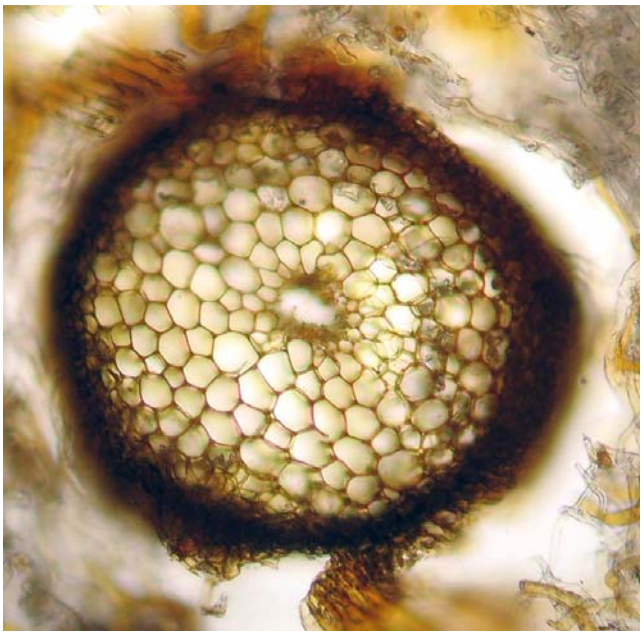

Figure 76. ***Dicranum scoparium*** stem cross section showing differentiated central tissue with hydroids, but representing a genus where leptoids are often absent. There appear to be hydroids that are breaking up, possibly surrounded by a narrow band of leptoids. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 77. ***Tetraphis pellucida*** seta cross section. In this case, most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 78. ***Tetraphis pellucida*** stem cross section. As in the seta (Figure 77), most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle but occupy a larger area than in the seta. Photo from Botany website, University of British Columbia, Canada, with permission.

Hébant (1977) pointed out that no electron microscope study existed on the histology of the conducting tissue of the capsule. He could offer little on its organization, stating that the conducting strand terminates shortly after it enters the capsule. In ***Funaria hygrometrica*** and ***Polytrichum commune*** the hydroids terminate within the capsule as a small ampulla, but such an ampulla is absent in ***Dawsonia***, ***Dendroligotrichum***, and ***Fissidens***.

Adaptation and Evolution

The hydroids and leptoids present interesting evolutionary implications, since it appears that they are primitive characters that are lost in more advanced bryophyte taxa (Hébant 1970; Behnke 1975). Unlike most tracheophytes, the mosses retain conducting cells in both generations, but the haploid generation is the first to lose leptoids evolutionarily, as in ***Funaria*** (Behnke 1975), a moss that still has a central strand in the stem (Malcolm & Malcolm 2006) and leptoids in its setae (Hébant 1977).

Being Acrocarpous

Some acrocarpous mosses may lack a central strand. For example, ***Leptodontium flexifolium*** (Figure 79-Figure 80) grows on acid substrata but lacks the central strand (Figure 80), but it has a leaf costa (Figure 79). Even the ubiquitous ***Ceratodon purpureus*** (Figure 81), a moss that occurs on substrata from roadsides and exposed rocks to pools in the Antarctic, lacks a central strand (Figure 82), and likewise has a costa (Figure 83-Figure 84). Other taxa that frequently become dry, like ***Grimmia*** species (Figure 85) also often lack specialized cells in the center of the stem (Hébant 1977).

Figure 79. ***Leptodontium flexifolium***, an acrocarpous moss. Photo by Des Callaghan, with permission.

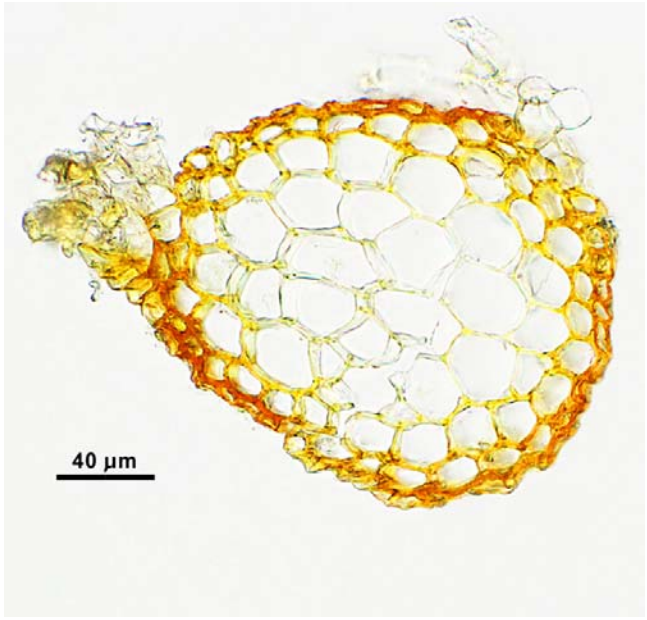

Figure 80. ***Leptodontium flexifolium*** stem cross section showing absence of hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

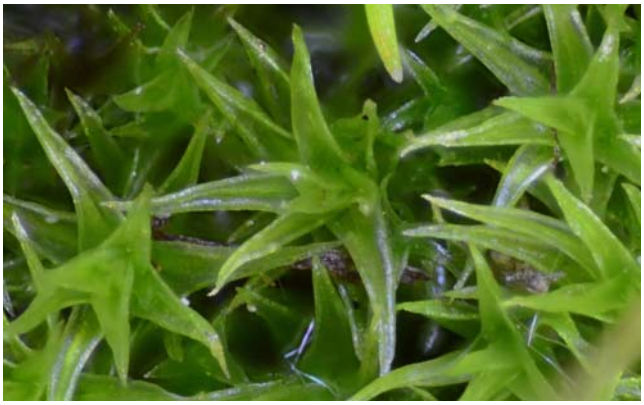

Figure 81. ***Ceratodon purpureus*** leaves. Photo by Don Loarie, through creative Commons.

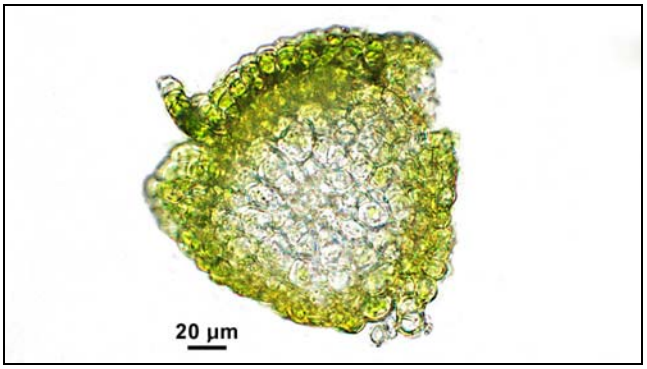

Figure 82. ***Ceratodon purpureus*** stem, a moss with a wide range of habitats from dry fields to Antarctic pools, yet it lacks hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 83. ***Ceratodon purpureus*** showing distinct costa. Photo by Malcolm Storey, through Creative Commons.

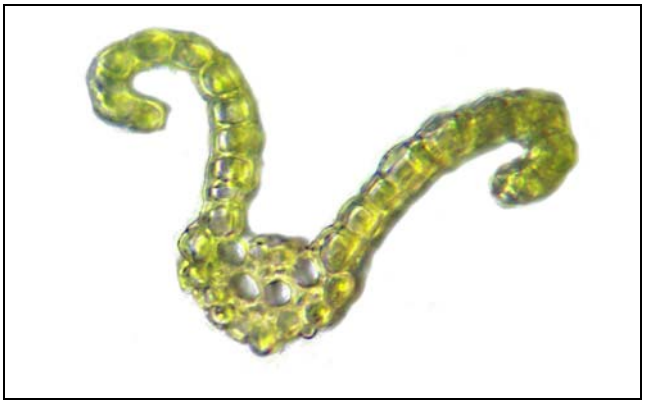

Figure 84. ***Ceratodon purpureus*** leaf cross section showing costa and involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 85. ***Grimmia pulvinata*** stem cross section showing little differentiation in the central cells of the cortex. Are these hydroids? This genus can have hydroids or lack them. The tissues flaking away from the stem are leaf cross sections. Photo from Botany website, UBC, with permission.

Being Pleurocarpous

Pleurocarpous taxa that grow close to the ground may have less need for hydroids when all their leaves are more or less equally placed to gain water, as can be seen in ***Calliergonella lindbergii*** (=*Hypnum lindbergii*; Figure 86). Pleurocarpous mosses (Figure 86-Figure 89) have fewer problems in getting wet and sharing water among cells because they grow horizontally, compared to the need for upright mosses to distribute water, especially tall ones that grow alone, like ***Dawsonia*** spp. (Figure 2). On the other hand, these mosses may have evolved the loss of hydroids before our extant species existed and have not regained their hydroids, as might be the case for ***Hylocomium splendens*** (Figure 88-Figure 89), a moss that grows in fairly open wefts, but lacks a central strand. Nevertheless, it would seem that the pleurocarpous mosses still need to transport photosynthate and hormones, among other things. Hence, we should expect leptoids in many, if not all, pleurocarpous mosses. Unfortunately, it is hard to find information on leptoids in these taxa. The same need, and lack of information, could be said for leafy liverworts.

Figure 86. ***Calliergonella lindbergii*** forming a thick mat. Photo by Michael Lüth, with permission.

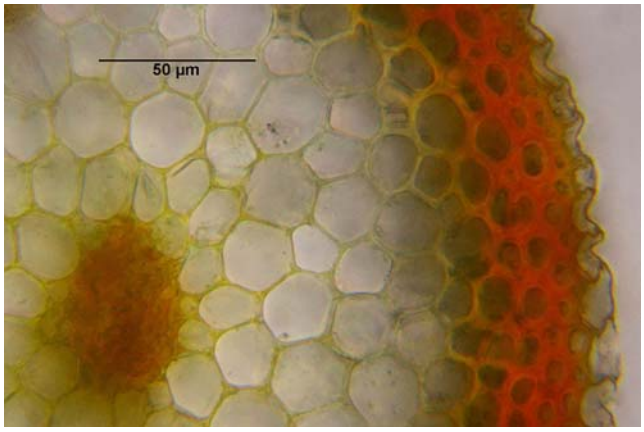

Figure 87. ***Calliergonella lindbergii***, a pleurocarpous moss, stem cross section showing a small area of differentiated central tissue. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Hylocomium splendens***, showing its open growth habit that will permit easy escape of water. This moss grows in an almost dendroid pattern, but together with many stems that form wefts. Photo by Dale Vitt, with permission.

Figure 89. ***Hylocomium splendens***, a pleurocarpous moss, stem cross section showing absence of any hydroids or central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

In ***Climacium*** (Figure 90), the stem has very reduced strands of conducting tissue (Hébant 1977). This moss stands upright like a small tree. The stem is nearly naked, making external upward transport limited. Hence this moss must rely on water that lands on the leaves. Instead of specialized water conducting cells, ***Climacium*** species have good supporting tissues in their stems, permitting the stem to support the leafy tree-like portion.

Figure 90. ***Climacium dendroides*** showing the nearly naked supporting stem. Photo by Keith Bowman, with permission.

Aquatic

It should be no surprise that aquatic taxa like ***Fontinalis*** (Figure 91-Figure 93) lack hydroids. Likewise, in ***Touwia*** (Figure 94), a pleurocarpous moss in the **Neckeraceae**, there is no cross-sectional evidence of a central strand (Figure 95). Rather, like ***Fontinalis***, this streambed moss has many thick-walled cortex cells that help to protect the stem from breakage in stream flow. Its leaves likewise have a thick **costa** (Figure 96) that can resist the ravages of flow. But even in such epiphytic taxa as ***Neckera crispa*** conducting cells are lacking, suggesting an evolutionary loss early in this branch. Taxa like ***Touwia*** with a strong costa but no conducting cells in the stem suggest that the costa cells that are elongate in a leaf where other cells are shorter may serve a function more important than conduction – that of supporting tissue, and may sometimes serve both functions. It is likely that they also have regenerative ability.

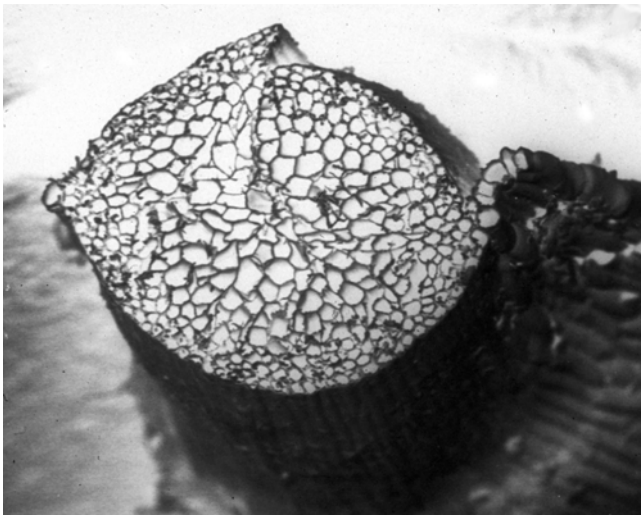

Figure 91. ***Fontinalis squamosa*** SEM image of stem cross section, showing the absence of specialized cells in the center of the stem. Photo by Janice Glime.

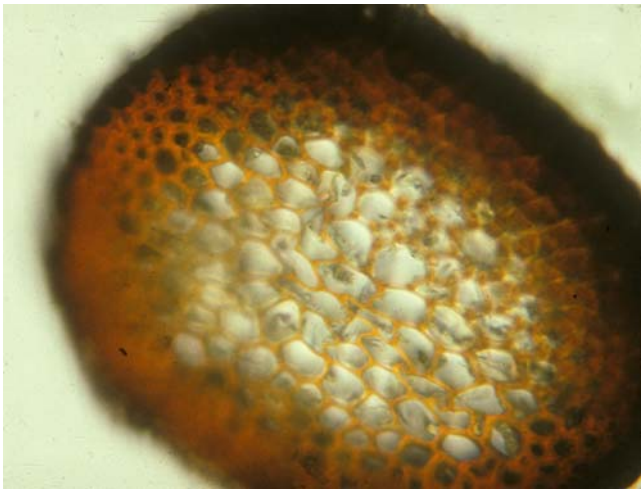

Figure 92. ***Fontinalis dalecarlica*** stem cross section showing absence of hydroids. Note the thick-walled outer cortical cells that give this stem the strength needed to survive in the rapidly flowing water of mountain streams. Photo by Janice Glime.

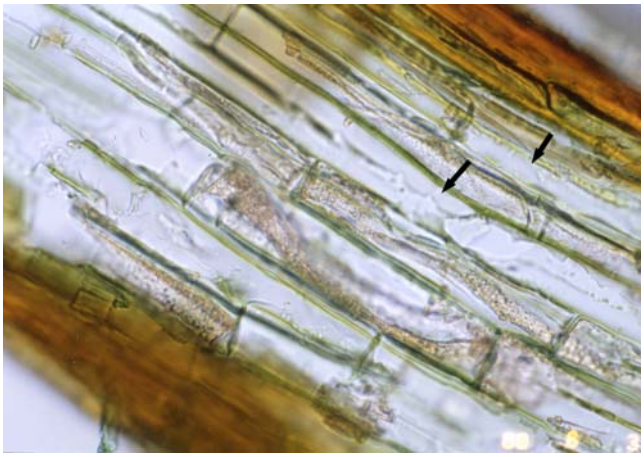

Figure 93. Longitudinal section of stem of ***Fontinalis gracilis*** showing elongated, thin-walled cells of the cortex. The cells at the arrows appear to be particularly long. Could they be leptoids? Photo by Isawo Kawai, with permission.

Figure 94. ***Touwia laticostata*** (?) branches showing leaves with thick costae. Note the remaining costae on the lower branch after it suffered abrasion. Photo courtesy of Andi Cairns.

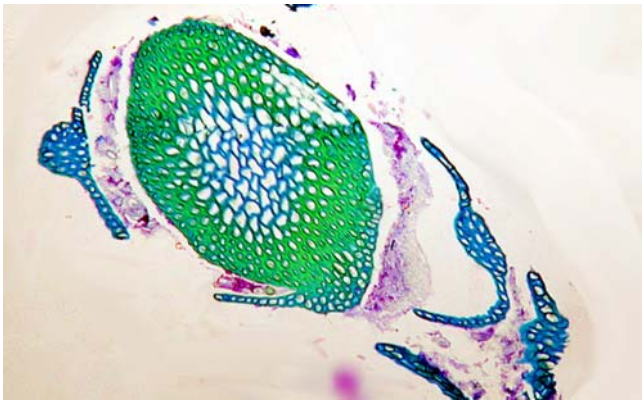

Figure 95. The moss ***Touwia laticostata*** (?) stem (lacking discernible hydroids) and leaves with thick costa. Photo courtesy of Andi Cairns.

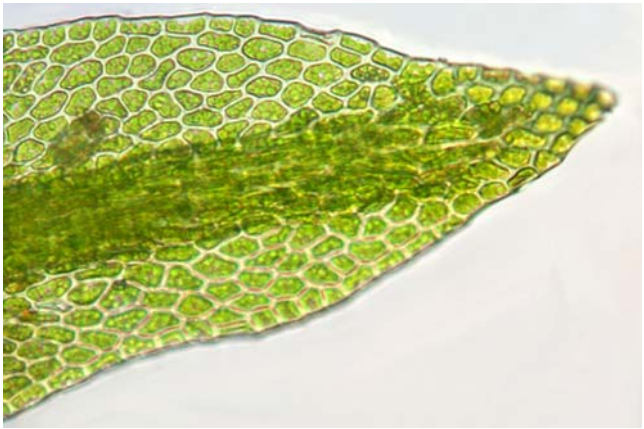

Figure 96. ***Touwia laticostata*** (?) leaf showing thick costa. Photo courtesy of Andi Cairns.

Using a Partner

Epiphyllous bryophytes have an unusual habitat on their host leaves. Water usually does not stay and is even repelled by the host leaf surface. ***Radula flaccida*** (Figure 97) has at least partially solved the problem by producing rhizoids that penetrate the host leaf cuticle and epidermal cells, extending into the tissues of the host (Berrie & Eze

1975). Berrie and Eze found that both water and dissolved phosphorus salts can be obtained from the host leaf. Hence, it appears that the liverwort is at least partially a parasite (Hébant 1977).

Figure 97. ***Radula flaccida*** habit with gemmae, growing on a leaf. Photo by Michaela Sonnleitner, with permission.

Throughout the kingdoms we see examples where two organisms share responsibilities in their mutual survival. Among these partners, the fungi seem to have perfected the strategy, making it possible for plants to greatly increase their available surface area without expending the effort to build the needed tissues. Such is the case for some bryophytes, a partnership for which we have limited understanding. Among those with such a relationship is the genus ***Haplomitrium*** (Figure 98) (Carafa *et al*. 2003). ***Haplomitrium*** secretes mucilage (Figure 99) from its underground rhizomes, forming an environment that harbors fungal hyphae. In ***H. gibbsiae*** (Figure 98), the fungus is restricted to the epidermal cells where it forms lumps, but in ***H. ovalifolium*** it also infects the adjacent cortical cells, forming lumps. Through such partnerships, these species can gain access to both deeper and wider sources of nutrients in the sol substrate.

In tracheophytes, this partnership strategy has been used by a number of **hemiparasites** that partner with a fungus that partners with a tree or shrub. This arrangement permits them to gain carbohydrate energy from the photosynthesizing canopy while living in the darker environment under its protective cover. Our knowledge of bryophyte partnerships is still too primitive to ascertain how important this relationship is in permitting many bryophytes to subsist in such low light conditions.

Figure 98. ***Haplomitrium gibbsiae*** leafy plant showing slimy rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.

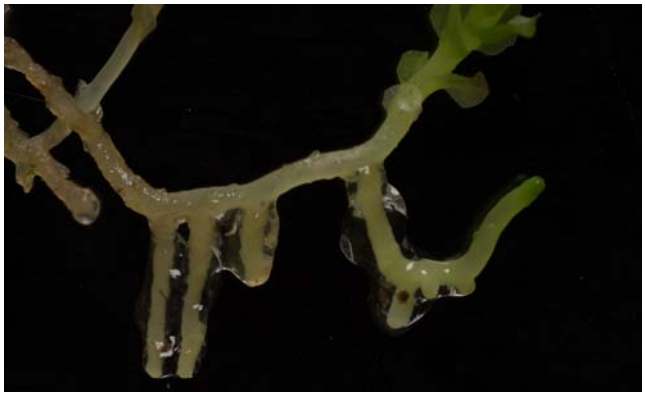

Figure 99. ***Haplomitrium gibbsiae*** rhizomes covered with thick mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

Summary

Movement onto land required means of obtaining and retaining water. Bryophytes, reputedly the first colonizers, often are not the nonvascular plants we once thought them to be. They often possess **hydroids**, surrounded by **stereids**, that conduct water and together comprise the **hydrome**. Hydroids lack lignin and spiral thickenings, distinguishing them from tracheids and vessels of tracheophytes. **Leptoids** that conduct sugars, arranged as in tracheophytes, with the water-conducting cells surrounded by the sugar-conducting cells, are less well known because they are distinguishable in longitudinal section. In a few mosses, these stem conducting tissues connect by leaf traces to the leaves. Bryophytes usually have a thin **cuticle**, but it seems to lack wax in most cases. **Rhizoids**, although anchoring the plants as do roots, typically do not serve in obtaining water, but exceptions exist. **Acrocarpous** species more commonly have a central conducting strand, whereas **pleurocarpous** mosses remain close to the substrate and a central strand may not be useful.

Bryophytes function like sponges in the ecosystem by holding water and maintaining moisture in the soil below. But they also absorb water like a sponge, using capillary spaces. At times when water is limiting, the bryophytes are able to survive through their exceptional desiccation tolerance.

Mosses may have a **costa** (rib similar to a midrib) in the leaf, but it does not branch to reach all the cells (as in most tracheophytes) and may not always serve a conduction role. This is connected to the stem vascular strands only in the **Polytrichaceae**. Thallose liverworts may have a midrib to transport water and other substances, but leafy liverworts have no evidence of water-conducting cells in the stem and no **costa** in the leaf.

Even sporophytes have elongated cells in the seta. In younger sporophytes these may be important in conduction of nutrients to the developing capsule.

Aquatic species presumably do not need conduction since they are bathed in water. But they still need to move solutes and especially sugars from leaves to other locations. Some bryophytes have mycorrhizal associates that help take in water and

minerals. Others are connected by rhizomes that permit them to "scavenge" by obtaining photosynthate from connected stems that are in more favorable positions.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who read the manuscript for clarity. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. Jean Faubert suggested problems in the original chapter and reviewed the revised chapter for me. Isawo Kawai sent me a large parcel of images of stained stem sections. Jeff Duckett and Silvia Pressel invited me to peruse their digital image library for images I could use.

Literature Cited

Anderson, L. E. and Bourdeau, P. F. 1955. Water relations in two species of terrestrial mosses. Ecology 36: 206-212.

Atala, C. and Alfaro, J. F. 2012. Vascular architecture of the dendroid antipodean moss *Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. (Polytrichaceae). J. Bryol. 34: 277-280.

Bassi, M. and Favali, M. A. 1973. Seta ultrastructure in *Mnium orthorhynchum*. Nova Hedwigia 24: 337-345.

Behnke, H.-D. 1975. Phloem tissue and sieve elements in algae, mosses and ferns. In: Aronoff, S., Dainty, J., Gorham, P. R., Srivastava, L. M., and Swanson, C. A. (eds.). Phloem Transport. Plenum Press, N. Y., pp. 187-210.

Berrie, G. K. and Eze, J. M. O. 1975. The relationship between an epiphyllous liverwort and host leaves. Ann. Bot. 39: 955-963.

Buch, H. 1945. Über die Wasser- und Mineralstoffversorgung der Moose (Part 1). Soc. Sci. Fenn., Comment. Biol. 9(16): 1-44.

Buch, H. 1947. Über die Wasser- und Mineralstoffversorgung der Moose. (Part 2). Soc. Sci. Fenn., Comment. Biol. 9(20): 1-61.

Buch, H., Evans, A. W., and Verdoorn, F. 1938. A preliminary check list of the Hepaticae of Europe and America (North of Mexico). Ann. Bryol. 10: 3-8.

Carafa, A., Duckett, J. G., and Ligrone, R. 2003. Subterranean gametophytic axes in the primitive liverwort *Haplomitrium* harbour a unique type of endophytic association with aseptate fungi. New Phytol. 160: 185-197.

Comis, D. 1992. Miracle moss: Add water and watch it grow. Agric. Res. 40(6): 10-11.

Cortella, A., Ron, E., Estébanez, B., and Alfayate, C. 1994. On the occurrence of primary pit field cells in the caulidia of *Hookeria lucens* (Hedw.) Sm. (Bryopsida, Bryophyta). J. Hattori Bot. Lab. 77: 287-294.

Crandall-Stotler, B. 1980. Morphogenetic designs and a theory of bryophyte origins and divergence. BioScience 30: 580-585.

Crandall-Stotler, B. and Stotler, R. E. 2000. Morphology and classification of the Marchantiophyta. In: Shaw, A. J. and Goffinet, B. (eds.). Bryophyte Biology, Cambridge University Press, Cambridge, UK, pp. 21-70.

Duckett, J. G. and Ligrone, R. 2003. What we couldn't have done if we'd stayed in Europe: Selection and serendipity in the Southern Hemisphere!. Bull. Brit. Bryol. Soc. 80: 19-21.

Edelmann, H. G., Neinhuis, C., Jarvis, M., Evans, B., Fischer, E., and Barthlott, W. 1998. Ultrastructure and chemistry of the cell wall of the moss *Rhacocarpus purpurascens* (Rhacocarpaceae): A puzzling architecture among plants. Planta 206: 315-321.

Edwards, D., Axe, L., and Duckett, J. G. 2003. Diversity in conducting cells in early land plants and comparisons with extant bryophytes. Bot. J. Linn. Soc. 141: 297-347.

Favali, M. A. and Gianni, F. 1973. Sporophyte ultrastructure in *Tortula muralis* Hedw. Österr. Bot. Zeit. 122: 323-331.

Frey, W. and Richter, U. 1982. Perforierte Hydroiden bei Laubmoosen? J. Hattori Bot. Lab. 51: 51-60.

Gray, J. 1985. The microfossil record of early land plants: Advances in understanding of early terrestrialization, 1970-1984. Phil. Trans. Roy. Soc. Lond. B 309: 167-195.

Hébant, C. 1969. Observations sur les traces foliaires des mousses *s. str*. (Bryopsida). I. Les hydroides et leurs relations avec le cylindre central. Rev. Bryol. Lichénol. 36: 721-728.

Hébant, C. 1970. A new look at the conducting tissues of mosses (Bryopsida): Their structure, distribution and significance. Phytomorphology 20: 390-410.

Hébant, C. 1973a. Acid phosphomonoesterase activities (β-glycerophosphatase and naphthol AS-MX phosphatase) in conducting tissues of bryophytes. Protoplasma 77: 231-241.

Hébant, C. 1973b. Diversity of structure of the water-conducting elements in liverworts and mosses. J. Hattori Bot. Lab. 37: 229-234.

Hébant, C. 1974. The phloem (leptome) of bryophytes. In: Aronoff, S., Dainty, J., Gorham, P. R., Srivastava, L. M., and Swanson, C. A. (eds.). Phloem Transport. Plenum Press, N. Y., pp. 211-215.

Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Lehre, Germany, 157 pp. + 80 Plates.

Hébant, C. 1978. Development of pores in water-conducting cells of the liverwort *Hymenophyton flabellatum* (Metzgeriales, Bryophytes). Protoplasma 96: 205-208.

Hedenäs, L. 1999. How important is phylogenetic history in explaining character states in pleurocarpous mosses? Can. J. Bot. 77: 1723-1743.

Kawai, I. 1971a. Systematic studies on the conducting tissue of the gametophyte in Musci (2). On the affinity regarding the inner structure of the stem in some species of Dicranaceae, Bartamiaceae (sic), Entodontaceae, and Fissidentaceae. Ann. Rept. Bot. Gard., Fac. Sci. Kanazawa Univ. 4: 18-40.

Kawai, I. 1971b. Systematic studies on the conducting tissue of the gametophyte in Musci (3). On the affinity regarding the inner structure of the stem in some species of Thuidiaceae. Sci. Rept. Kanazawa Univ. 16(1): 21-60.

Kawai, I. 1971c. Systematic studies on the conducting tissue of the gametophyte in Musci (4). On the affinity regarding the inner structure of the stem in some species of Mniaceae. Sci. Rept. Kanazawa Univ. 16(2): 83-111.

Kawai, I. 1976. Systematic studies on the conducting tissue of the gametophyte in Musci (6). On the essential coordination among the anatomical characteristics of the stem in some species of Hypnaceae. Sci. Rept. Kanazawa Univ. 21(1): 47-124.

Kawai, I. 1977a. Die systematische Forschung auf Grund der Zellteilungsweise für die Bryophyten II. Die Zellteilungsweisen der Gametophyten in der

Lebensgeschichte (1). *Climacium*. Sci. Rept. Kanazawa Univ. 22: 45-90.

Kawai, I. 1977b. Systematic studies on the conducting tissue of the gametophyte in Musci (7). On the essential coordination among the anatomical characteristics of the stems in the some species of Isobryales. Sci. Rept. Kanazawa Univ. 22(2): 197-305.

Kawai, I. 1978. Systematic studies on the conducting tissue of the gametophyte in Musci (8). On the essential coordination among the anatomical characteristics of the stems in some species of Amblystegiaceae. Sci. Rept. Kanazawa Univ. 23(2): 93-117.

Kawai, I. 1979. Systematic studies on the conducting tissue of the gametophyte in Musci (9). On regularity among anatomical characteristics of stems in some species of Dicranaceae. Sci. Rept. Kanazawa Univ. 24(1): 13-43.

Kawai, I. 1980a. Anatomical characteristics of stems in some species of Dicranaceae. Proc. Bryol. Soc. Japan 2: 126.

Kawai, I. 1980b. Systematic studies on the conducting tissue of the gametophyte in Musci (11). Anatomical characteristics of stems in some species of Leucobryaceae. Sci. Rept. Kanazawa Univ. 25(1): 31-42.

Kawai, I. 1981. Systematic studies on the conducting tissue of the gametophyte in Musci (10). Organization of the stem and its origin. Hikobia (Suppl.) 1: 29-33.

Kawai, I. 1982. Systematic studies on the conducting tissue of the gametophyte in Musci (12). Anatomical characteristics of stems in some species of Bartramiaceae. Sci. Rept. Kanazawa Univ. 26: 31-50.

Kawai, I. 1989. Systematic studies on the conducting tissues of the gamestophyte [sic] in Musci: XVI. Relationships between the anatomical characteristics of the stem and the classification system. Asian J. Plant Sci. 1: 19-52.

Kawai, I. 1991a. Systematic studies on the conducting tissue of the gametophyte in Musci (18). On the relationship between the stem and the rhizome. Ann. Rept. Bot. Gard., Fac. Sci. Kanazawa Univ. 14: 17-25.

Kawai, I. 1991b. Systematic studies on the conducting tissue of the gametophyte in Musci (19). Relationships between the stem and seta in some species of Polytrichaceae, Bryaceae, Mniaceae, Bartramiaceae and Dicranaceae. Sci. Rept. Kanazawa Univ. 36(1): 1-19.

Kawai, I. and Ikeda, K. 1970. Systematic studies on the conducting tissue of the gametophyte in Musci. (1) On the affinity regarding the conducting tissue of the stem in some species of Polytrichaceae. Sci. Rept. Kanazawa Univ. 15(2): 71-98.

Kawai, I. and Ochi, H. 1987. Systematic studies on the conducting tissues of the gametophyte in Musci (15). Relationships between the taxonomic system and anatomical characteristics of stems in some species of Bryaceae. Sci. Rept. Kanazawa Univ. 32(1): 1-67.

Kawai, I., Yoshitake, S., and Yamazaki, M. 1985. Systematic studies on the conducting tissue of the gametophyte in Musci (13). Anatomy of the stem through analysis of pigment deposition in *Polytrichum commune* Hedw. and *Pogonatum contortum* (Brid.) Lesq. Sci. Rept. Kanazawa Univ. 30: 47-53.

Kawai, I., Yoshitake, S., and Yamamoto, E. 1986. Systematic studies on the conducting tissue of the gametophyte in Musci (14). Anatomy of the stems of *Rhizogonium*, *Mnium*, and *Fissidens*. Sci. Rept. Kanazawa Univ. 21(1,2): 31-42.

Lawrey, J. D. 1977. Litter decomposition and trace metal cycling studies in habitats variously influenced by coal strip-mining. Ph. D. dissertation. Ohio State University, Columbus.

Ligrone, R. and Duckett, J. G. 1994. Cytoplasmic polarity and endoplasmic microtubules associated with the nucleus and organelles are ubiquitous features of food conducting cells in bryalean mosses (Bryophyta). New Phytol. 127: 601-614.

Ligrone, R. and Duckett, J. G. 1998. The leafy stems of *Sphagnum* (Bryophyta) contain highly differentiated polarized cells with axial arrays of endoplasmic microtubules. New Phytol. 140: 567-579.

Ligrone, R., Duckett, J. G., and Renzaglia, K. S. 2000. Conducting tissues and phyletic relationships of bryophytes. Philosoph. Trans. Royal Soc. B: Biol. Sci. 355: 795–813.

Ligrone, R., Vaughn, K. C., Renzaglia, K. S., Knox, J. P., and Duckett, J. G. 2002. Diversity in the distribution of polysaccharide and glycoprotein epitopes in the cell walls of bryophytes: New evidence for the multiple evolution of water-conducting cells. New Phytol. 156: 491-508.

Malcolm, B. and Malcolm, N. 2006. Mosses and Other Bryophytes: An Illustrated Glossary 2nd ed. Micro-optics Press, New Zealand, 336 pp.

Niklas, K. J. 1976. Plant evolution and the reciprocity model. Ann. Bot. 40: 1255-1264.

Oliver, M. J., Tuba, Z., and Mishler, B. D. 2000a. The evolution of vegetative desiccation tolerance in land plants. Plant Ecol. 151: 85-100.

Oliver, M. J., Velten, J., and Wood, A. J. 2000b. Bryophytes as experimental models for the study of environmental stress tolerance: *Tortula ruralis* and desiccation-tolerance in mosses. Plant Ecol. 151: 73-84.

Pressel, S., P'ng, K. M. Y., and Duckett, J. G. 2010. A cryo-scanning electron microscope study of the water relations of the remarkable cell wall in the moss *Rhacocarpus purpurascens* (Rhacocarpaceae, Bryophyta). Nova Hedwigia 91: 289-299.

Proctor, M. C. F. 2000a. Mosses and alternative adaptation to life on land. New Phytol. 148: 1-6.

Proctor, M. C. F. 2000b. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Puckett, K. J. 1988. Bryophytes and lichens as monitors of metal deposition. In: Nash, T. H. III. and Wirth, V. (eds.), Lichens, Bryophytes and Air Quality. Biblioth. Lichenol. 30: 231-267.

Raven, J. A. 2002. Commentary: Putting the fight in bryophytes. New Phytol. 156: 321-323.

Raven, J. A. 2003. Long-distance transport in non-vascular plants. Plant Cell Environ. 26: 75-85.

Richardson, D. H. S. 1981. The Biology of Mosses. John Wiley & Sons, Inc., N. Y., 220 pp.

Ron, E. and Kawai, I. 1990. Systematic studies on the conducting tissue of the gametophyte in Musci (17). On the relationships between the stem and the rhizome (forecast). Ann. Rept. Bot. Gard., Fac. Sci. Kanazawa Univ. 13: 15-18.

Scheirer, D. C. 1973. Hydrolysed walls in the water-conducting cells of *Dendroligotrichum* (Bryophyta): Histochemistry and ultrastructure. Planta 115: 37-46.

Scheirer, D. C. 1975. Anatomical studies in the Polytrichaceae. II. Histochemical observations on thickened lateral walls of hydroids of *Dendroligotrichum*. Bryologist 78: 113-123.

Scheirer, D. C. 1980. Differentiation of bryophyte conducting tissues: Structure and histochemistry. Bull. Torrey Bot. Club 107: 298-307.

Scheirer, D. C. and Goldklang, I. J. 1977. Pathway of water movement in hydroids of *Polytrichum commune* Hedw. (Bryopsida). Amer. J. Bot. 64: 1046-1047.

Schimper, W. Ph. 1857. Mémoire pour servir à l'histoire naturelle des Sphaignes. Paris. 96 pp.

Schnepf, E. Mikrotubulus-Anordnung und –Umordnung, Wandbildung und Zellmorphogenese in jungen *Sphagnum*-Blättchen. Protoplasma 78: 145-173.

Smith, J. L. 1964. Water conducting system of *Symphogyna.* Nature 202: 617.

Tansley, A. G. and Chick, E. 1901. Notes on the conducting tissue system in the Bryophyta. Ann. Bot. 15: 1-39.

Taylor, T. N. 1988. The origin of land plants: Some answers, more questions. Taxon 37: 805-833.

Vanderpoorten, A. and Goffinet, B. 2009. Introduction to Bryophytes. Cambridge University Press, Cambridge, 303 pp.

Zamski, E. and Trachtenberg, S. 1976. Water movement through hydroids of a moss gametophyte. Israel J. Bot. 25: 168-173.

CHAPTER 7-2

WATER RELATIONS: MOVEMENT

TABLE OF CONTENTS

Water Movement 7-2-2
Ectohydric 7-2-3
Endohydric 7-2-5
Nocturnal 7-2-7
Mechanisms of Water Movement 7-2-8
Transport to Sporophyte 7-2-9
Summary 7-2-10
Acknowledgments 7-2-10
Literature Cited 7-2-10

CHAPTER 7-2
WATER RELATIONS: MOVEMENT

Figure 1. *Grimmia nutans* supporting drops of water that will eventually be absorbed into the moss through the leaf surface. Photo by Michael Lüth, with permission.

Water Movement

Early experiments with dyes demonstrated that in mosses water is able to move in conducting tissue of the central cylinder, leaf traces, and the costa (Zacherl 1956), depending on capillary spaces, as it does in tracheophytes (Table 1). Bopp and Stehle (1957) confirmed not only these internal pathways, but that movement also occurs from cell to cell (**symplastic**) in the cortex of the lower part of the stem, as well as on the outer surfaces of leaves and stems (Figure 1). But it is more likely that most of the movement across the cortex and internal leaf is through the free space of the cell walls where it does not have to cross cell membranes until it reaches its destination (Proctor 1984). Such **apoplastic** (outside cell membrane or in free space) movement across the cortex is known even in ***Polytrichum juniperinum*** (Figure 2) (Trachtenberg & Zamski 1979), where a central strand and leaf traces are available to facilitate movement of water.

Table 1. Relationship of bryophyte structures, size of space, and capillary rise. From Proctor (1982), based on Slatyer (1967).

Radius of meniscus	Ht of capillary rise	Bryophyte structures in similar size range
1 mm	1.5 cm	Large, concave leaves; spaces among shoots
100 µm	15 cm	Spaces between leaves, paraphyllia
10 µm	1.5 m	Space within sheathing leaf base, tomentum, hyalocyst of ***Sphagnum*** & ***Leucobryum***
1 µm	15 m	Interstices between leaf-surface papillae
100 nm	150 m	Spaces between cell-walls?
10 nm	1.5 km	Spaces between cell-wall microfibrils
1 nm	15 km	Glucose molecule

As in tracheophytes, water movement in both endohydric and ectohydric mosses is facilitated by tension forces (Zamski & Trachtenberg 1976), but unlike the case in tracheophytes, water moves in both directions in a source-sink fashion dependent upon availability (Bowen

1933a). This bi-directional movement applies not only to external movement, but to the hydrome as well. For bryophytes, the first water availability most commonly does not start with the soil, but with the tips of stems and leaves by way of rain, fog, or dew.

Figure 2. ***Polytrichum juniperinum***, a moss with good **symplastic** conduction, but that can also use apoplastic movement. Photo by Des Callaghan, with permission.

Early observations showed that in general external conduction is much more rapid than internal conduction (Bowen 1933a, b, c; Clee 1939). This most likely relates to frictional resistance in the small internal routes. On the other hand, we should expect water to rise higher in small internal capillary spaces (Table 1). What seems strange, however, is that the utility of internal conduction in at least some bryophytes can change with age toward greater use of external conduction. Mizushima (1980) found that in older stems of ***Entodon rubicundus*** no internal conduction could be detected at 75% atmospheric humidity, but in younger stems, a slow internal conduction could be detected in the **central strand**. Both young and old stems exhibited external conduction, travelling up to 1 cm in 12 hours. This loss of internal conduction in older plants may support the contention of Kawai (1991), among others, that mosses may have been derived from vascular plants by reduction.

One item of curiosity is that not all bryophytes have **vacuoles** (Oliver & Bewley 1984). Surely this plays some role in their ability to hold water, and most likely affects nutrient placement and protection from toxic substances as well, but no one seems to have looked at this role in bryophyte physiology (Bates 2000).

Ectohydric

Ectohydric mosses (almost all mosses) rely primarily on external transport of water and can absorb water over the entire plant surface (Figure 3). These taxa generally have no water repellent layers, or these are restricted to such locations as the apices of papillae, and they are easily wetted (Proctor 1982, 1984). Movement is due to capillarity and the relationships are complex. As the moss becomes hydrated, its capillarity changes due to expansion of leaves, untwisting, and other forms of movement and gyration (Deloire *et al*. 1979). They benefit from a large surface area relative to their volume (Proctor 1984) due to numerous leaves and often such structures as **paraphyllia** (reduced leaflike structures on the stem or branches of some pleurocarpous mosses) and **tomentum** (felt-like covering of abundant rhizoids on stem).

Figure 3. Capillary water (**arrow**) held among the leaves of ***Bryum***. Photo courtesy of John Hribljan.

Castaldo Cobianchi and Giordano (1984) concluded that in the ectohydric ***Zygodon viridissimus*** (var. *rupestris*) (Figure 4-Figure 5), having an apical cell with no surface wax or papillae might provide a "starting-point" for rehydration since the dry leaves are appressed to the stem. When water repellent layers are lacking, plants generally reach full hydration within minutes (During 1992). Thus, virtually all pleurocarpous mosses, many of acrocarpous mosses, and most of leafy liverworts are readily wet by the first few minutes of rain. You will soon know which ones are resistant to uptake by leaves because they will stubbornly refuse to rehydrate for you when you want to make a leaf slide. Only dousing in boiling water seems to coax the water inside the plant to restore its normal hydrated shape.

Figure 4. ***Zygodon viridissimus*** dry showing leaves appressed to stem. Photo by Michael Lüth, with permission.

Figure 5. ***Zygodon viridissimus***, a moss in which the apical cell of the leaf lacks wax, permitting water entry. Photo by David Holyoak, with permission.

The **ectohydric** habit depends on entry of water through the moss surface and permits a moss to respond to dew and fog by absorbing water directly, even though rooted plants may never receive a drop of it. Such bryophytes can live in high elevations and on deserts that receive less than 25 cm rainfall per year, obtaining water that cannot be measured by conventional precipitation methods. Most tuft-forming (acrocarpous) mosses are (partially) endohydric, whereas most mat and carpet formers (pleurocarpous mosses) are ectohydric (Richardson 1981). In addition, some upright mosses such as ***Sphagnum*** (Figure 6) and ***Andreaea*** (Figure 7) are ectohydric. Schipperges and Rydin (1998) clearly showed this by clipping the capitula from the stem; these clipped capitula were unable to recover from desiccation, whereas unclipped capitula became rehydrated. But Even ***Sphagnum*** has highly specialized cells in the stem that have all the traits of a bryophyte type of conducting cell (Ligrone & Duckett 1998).

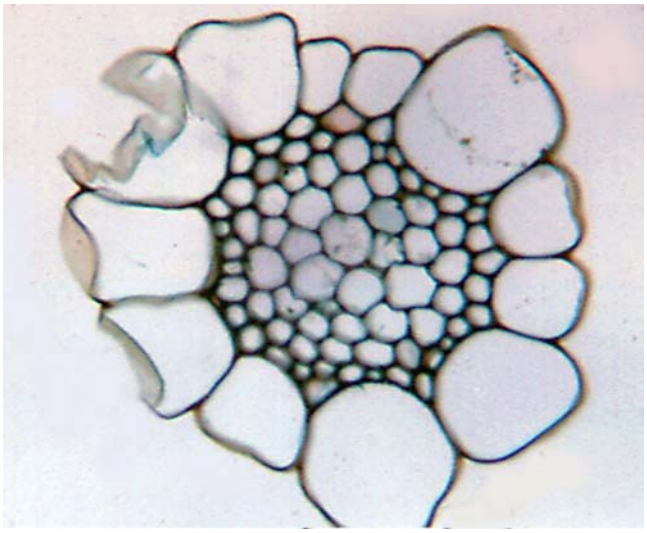

Figure 6. Cross section of ***Sphagnum*** stem with large, hyaline epidermal cells and small cortex cells. Photo by Janice Glime.

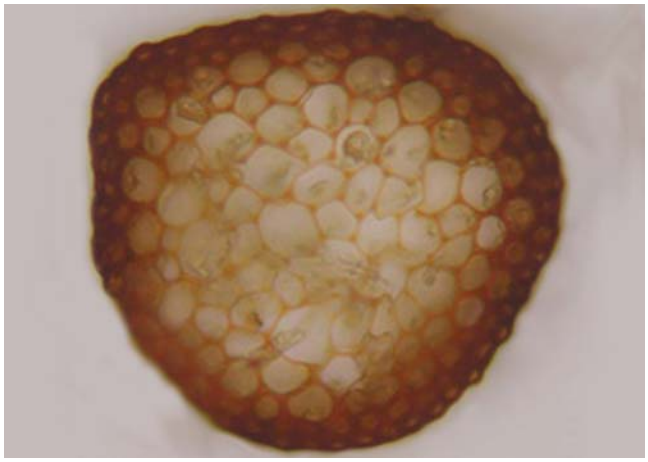

Figure 7. Cross section of ***Andreaea*** stem with no central strand. Photo from Biology 321 Course Website, University of British Columbia, with permission.

In **ectohydric** bryophytes, the uppermost leaves and shoot apices have the most rapid conduction of water, so that lower leaves are often supplied last (Zacherl 1956). Zacherl believed that no internal conduction was possible in the absence of a central strand. This apical movement may be beneficial in conserving water when water is scarce and only the leaves at the tips of the stems are receiving enough light for photosynthesis. These also are the leaves most exposed to fog and dew.

Using dyes and ***Dicranum scoparium*** (Figure 8) as a model subject, Bowen (1933c) demonstrated that external conduction was "exceptionally rapid" and internal conduction slow. Mägdefrau (1935), using the same species, determined internal conduction to be only about 1/3 the total conduction – not bad for a bryophyte. Klepper (1963) found that under conditions of desiccation, the protoplasts of this species become dense and evacuolate, undoubtedly developing considerable **imbibitional pressure** (due to adsorption of water by colloidal particles, much as seeds do. This would cause them to readily take in water when it becomes available.

Figure 8. ***Dicranum scoparium***. Photo by Michael Lüth, with permission.

Once the water enters the plant the distinction between endohydric and ectohydric no longer matters. Although the initial movement of water is clearly ectohydric in most dry mosses, once it has entered the moss it has the opportunity to move apoplastically to reach places where it is needed

for cellular metabolism. It is interesting that endohydric bryophytes can be facultatively ectohydric. Bayfield (1973) found that ***Polytrichum commune*** (Figure 9) was ectohydric under moderate moisture flux, but under high evaporative flux (*i.e.* dry air) it was predominantly endohydric.

Figure 9. ***Polytrichum commune***, a moss that is ectohydric under moderate moisture flux but endohydric under dry air. Photo by George Shepherd, through Creative Commons.

Despite all the laboratory experiments on conduction, we still have little concept of the relative importance of the two pathways over a large time scale in nature. Certainly, as demonstrated in ***Polytrichum*** (Figure 9), the relationship changes as the moss dries. Is it not likely that internal movement of water from older to younger parts then predominates, keeping the photosynthetic and growing apical tissue wet as long as possible? Surely the same apoplastic routes available to ***Polytrichum*** are available to all mosses. The natural transpirational stream that carries water from the shoot apices to the atmosphere could be expected to play a similar role to that found in tracheophytes and maintain upward movement (or outward in pleurocarpous mosses) through capillary spaces as long as water was available and internal tension did not exceed that resulting from transpirational loss.

What quantities do the various mosses move from moss mat to atmosphere and how much is moved from the soil to the moss mat? Do the mosses provide an overall net gain to the soil by preventing rapid loss to the atmosphere following rainfall? Do they retain water that would otherwise be lost as runoff, contributing it slowly to the soil and plant roots beneath? Or is their major contribution that of depriving the soil of water during showers of short duration? There is no mass balance equation that includes the role of bryophytes in the overall water budget in any ecosystem.

Endohydric

Endohydric mosses, including ***Polytrichum*** (Figure 2, Figure 9, Figure 13), ***Mnium*** *s.l.* (Figure 10,Figure 17), and ***Bryum*** (Figure 3), generally have surfaces that contain a water-resistant cuticle (Lorch 1931; Buch 1945; Bayfield 1973; Proctor 1979a), thus reducing their ability to take in water through their leaves. In some of these, that cuticle is endowed with a wax similar to that found in tracheophytes (Proctor 1979b; Haas 1982). However, this waxy coating of a moss leaf offers only a low water diffusion resistance similar to that of tracheophyte mesophyll (Nobel 1977; Proctor 1980) and may be more important in repelling water to permit a higher CO_2 diffusion into the leaf (Proctor 1984). Among ectohydric mosses, waxy cuticles seem to be either generally lacking or very thin. Mosses like ***Polytrichum*** and many members of the Marchantiales are actually water repellent, thus requiring half an hour or more to take up water (Proctor 1984). These **endohydric** bryophytes utilize, in the case of mosses, the system of non-lignified **hydroids** and **leptoids** to conduct water and sugars, respectively.

Figure 10. ***Mnium spinosum*** with water droplets on its leaves. This moss is very slow to absorb water due to its water-resistant cuticle. Photo by Michael Lüth, with permission.

But it appears that even these endohydric mosses rely on ectohydric transport. Instead of moving water inside the moss at the first opportunity during its external vertical rise, it is the tips of the plants that exhibit primary water absorption (Brown 1982). Water travels upward through the capillary spaces created by the leaves. Mosses like ***Polytrichum*** may facilitate this apical absorption by preventing any significant absorption by the cuticularized lower and more mature leaves.

In these predominantly endohydric mosses, rhizoids may serve functions of conduction much as do roots and root hairs. It appears that endohydric mosses such as ***Polytrichum*** (Figure 2, Figure 9, Figure 13), ***Dawsonia*** (Figure 11), and ***Climacium*** (Figure 12) transport water from the substrate beneath to their tips before moving it through an internal conducting system, sometimes called the **central strand**. Although ***Polytrichum commune*** (Figure 9) has demonstrated the ability to transport water externally along its stems, Mägdefrau (1938) contended that the major conduction is internal through the central strand. However, Trachtenberg and Zamski (1979) determined that despite the ability of rhizoids to absorb and transmit water, the major absorption is still through the aerial gametophyte, due to its greater efficiency. Because of the extensive development of conduction cells in ***Polytrichum*** (Figure 13), where central **hydroids** are surrounded by a cylinder of **leptoids**, Hébant (1970) considers this and other mosses to have similarities to the xylem and phloem of primitive vascular plants.

Figure 11. ***Dawsonia polytrichoides***, a moss with good internal conduction. Photo by Niels Klazenga, with permission.

Figure 12. ***Climacium dendroides***, a moss with external conduction from base to tip. Photo by Jan-Peter Frahm, with permission.

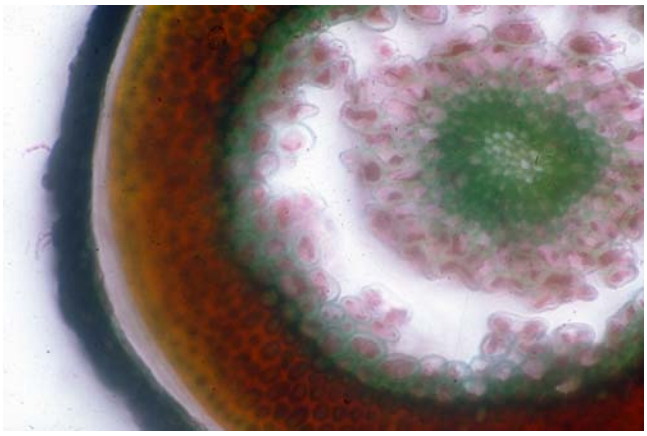

Figure 13. Cross section of a ***Polytrichum*** stem showing green **hydroids** of the **central strand** in center and larger **leptoids** surrounding them. Photo by Isawo Kawai, with permission.

But how does the water reach the leaves in the **endohydric** mosses? Zacherl (1956) used fluorescent dyes to show that in ***Polytrichum*** (Figure 2, Figure 9, Figure 13), the **costa** (midrib-like structure) links with the central strand, forming true leaf traces. In many taxa, however, there is no connection between the central strand and the costa, and in some cases there is no costa at all. Furthermore, Colbert (1979) showed that there is no connection between the central strand of the stem and that of the branches in ***Climacium americanum*** (Figure 14), ***C. dendroides*** (Figure 12), ***Rhytidiadelphus triquetrus*** (Figure 15), and ***Rhytidium rugosum*** (Figure 16).

Figure 14. ***Climacium americanum***, a moss with a central strand with no connection to the leaf. Photo by Bob Klips, with permission.

Figure 15. ***Rhytidiadelphus triquetrus***, a moss with a central strand that does not connect to the leaves. Photo by Janice Glime.

Figure 16. ***Rhytidium rugosum***, a moss with a central strand that does not connect to the leaves. Photo by Michael Lüth, with permission.

Nevertheless, in the absence of those connections the extension of the costa into the stem cortex still can function to complete internal transport across normal cortical cells (Zacherl 1956). For example, in ***Mnium*** (Figure 10) the costa does not link directly with the central strand of the stem, but ends blindly in the ground tissue, forming **false leaf traces** (Figure 17). The ends of the costae (Figure 18) act as wicks, transferring liquids across the ground tissue from the central strand and into the leaf costa, most likely using a diffusion gradient across the cortex.

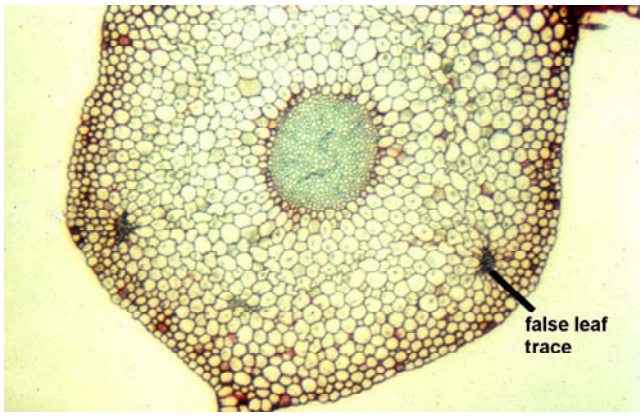

Figure 17. Cross section of ***Mnium*** stem showing false leaf traces. Photo by Janice Glime.

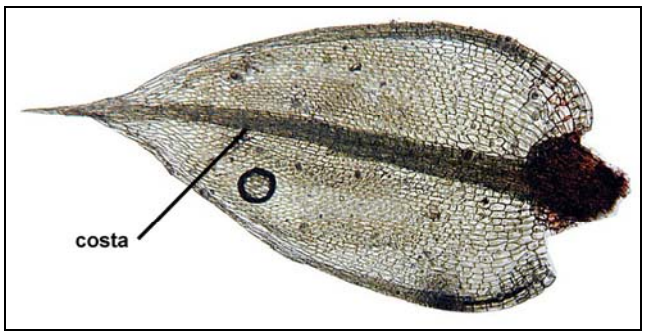

Figure 18. Leaf of ***Bryum pallescens***, showing costa of conducting cells. Photo by Michael Lüth, with permission.

The cortex behaves as capillary tubes and draws the water across the stem parenchyma to the leaf, much as water traversing the roots of tracheophytes. Trachtenberg and Zamski (1979) demonstrated, using PbS and Pb-EDTA (which accumulates Pb ions in tissues in proportion to the amount of water passing through), that the water actually moves in the capillary spaces of the cell walls – **apoplastic conduction**. Beckett (1997), using pressure volume isotherms, determined that cryptogams, including bryophytes, contain significant amounts of intercellular water when fully hydrated, whereas flowering plants do not. It is this extracellular pathway that permits water to move from leaf surfaces inward and into stems, where it can be conducted in the hydrome as well as apoplastically. It is interesting that the uppermost leaves are the first ones to receive water internally (Zacherl 1956), just as in the ectohydric mosses.

Trachtenberg and Zamski (1979) further learned that the **sterome**, assumed to be supporting tissue, can provide an alternative pathway for water conduction. That its mass was much greater than needed for support had already been noted by Lorch (1931). Furthermore, xerophytic mosses have a very large sterome (Goebel 1915) that is used for conducting and holding water. In mosses such as Fabroniaceae and Orthotrichaceae that lack a hydrome, the sterome is large (Van der Wijk 1932) and seems to supply this function. In fact, Trachtenberg and Zamski (1979) suggest that the transport from hydrome to leaves in ***Mnium*** (Figure 17) may take place through stereids. They support their hypothesis by demonstrating that the lead chelate solution applied to the leaves penetrates the sterome. They suggest that the most probable means of translocation of water from leaves into the stem is through the dense mass of stereids in leaves and leaf bases to the central cells of leaves and leaf traces to the hydrome. But only in the Polytrichaceae does there seem to be a connection between the leaf traces and both the leaf and hydrome. Rather, the apoplastic route through cell walls in the stem cortex is a more likely route in most cases.

Mixohydric bryophytes are those in which both endohydric and ectohydric methods are important. Many of the species in this group are small, acrocarpous mosses of loams or clays. These soils dry out frequently, but their fine texture permits them to maintain a moist top layer for a period of time after rain. Hébant (1977) contends that truly mixohydric mosses are not very abundant, implying that the ectohydric pathway is far more important in most. However, in reality, most (perhaps all) mosses are mixohydric in that they have both internal and external means of conduction to at least some degree.

Nocturnal

For many mosses, nighttime is the only period of rehydration. This is especially true for desert mosses such as ***Syntrichia ruralis*** (Figure 19). Csintalan *et al*. (2000) found that this moss obtained sufficient water through nighttime dew to accomplish 1.5 hours of net photosynthetic gain immediately after dawn. They suggested that such early morning periods might permit regular molecular repair due to desiccation damage during prolonged dry periods.

Figure 19. ***Syntrichia ruralis***. Photo by Michael Lüth, with permission.

But it appears that desert habitats are not the only places where nighttime moisture benefits the bryophytes. Carleton and Dunham (2003) contended that the uppermost growing tips of mosses could not be hydrated by simple capillary movement of water from the forest floor in the boreal forest. Rather, even in this mossy habitat, they

showed a nocturnal gain in mass due to vapor from the forest floor. As the forest floor cooled at night, distillation occurred with moisture condensing on the moss surface. The cooling temperatures and moisture provided by the forest floor was sufficient to cause the moss tips to reach dew point. This seems to be most evident in late summer when the lower organic layers have warmed the most and the surface temperature is thus relatively lower at night, causing the condensation. When a vapor barrier was used to prevent ground water from rising, no mass gain was in evidence.

Mechanisms of Water Movement

Bopp and Stehle (1957) found that a mechanism similar to the diffusion pressure deficit seen in higher plants worked in moving water up the moss. By using fluorescent dyes, Bopp and Stehle showed that water moved up the leafy gametophyte both internally and externally, but that dye went quickly to the foot of the sporophyte imbedded in the gametophyte, then moved up the seta through the central strand. In mosses with the calyptra removed, the flow rate increased, suggesting that transpiration loss may perform a function of pulling water, similar to that found in tracheophytes. Maier-Maercker (1982b) found an accumulation of radio-labelled and heavy metal ions in the annulus of the moss ***Plagiomnium cuspidatum*** (Figure 20), similar to that found in tracheophyte guard cells, suggesting that this area may be one of transpirational water loss.

Figure 20. ***Plagiomnium cuspidatum*** capsules showing annulus **arrows**) where labelled metal ions accumulated, suggesting a site of transpiration loss. Photo by Robert Klips, with permission.

Although bryophytes lack leaf stomata, they do lose water through their wax-free leaves. For example, the transpirational loss rates of the moss cover in the lichen tundra (16-20% of total precipitation) is not unlike that from the ericaceous shrubs of the tundra heath (24-26%) or the alpine dwarf shrub heath (16-20%), whereas tracheophytes in a wet meadow can have 135% loss (Larcher 1983 – data from many authors).

Using mosses from five different habitats ranging from wet to dry, Bowen (1933a,b,c) determined that the water ascends the mosses as capillary films between the leaves and stem, being absorbed at the stem and branch apices by the younger cells with unthickened walls. From there it diffuses through internal tissues laterally, then downward, not upward as in tracheophytes. Conduction from the base through the central strand is slow in cut stems but much slower when the stem base is still intact (Bowen 1933a,b,c). In the latter case, water must penetrate the thick walls of the rhizoids and stem/rhizome. And at least some of the species have cuticles on the rhizoids!

Once water reaches the central strand, it travels there preferentially (Hébant 1977). Internal ascending water travels through the narrow, elongated, thin-walled cells (presumably hydroids). In addition to apical absorption, leaves and stem epidermis absorb some of the water, albeit less readily due to cell-wall thickening and cuticles.

The capacity of both internal and external water conduction seems to diminish as the moisture of the habitat increases (Bowen 1933a, b, c). Mägdefrau (1935) contends that at 90% humidity, ***Polytrichum*** (Figure 2, Figure 9, Figure 13) can maintain its turgor with internal conduction only, but at 70% both internal and external conduction are necessary. For all other families of mosses, with the possible exception of the Mniaceae, a significant amount of external conduction seems necessary.

Vitt (1990) suggests that those mosses that must endure a greater range of fluctuations in water availability may be more plastic in their responses. At least among the boreal mosses, the ectohydric, drought-tolerant ***Hylocomium splendens*** exhibits highly variable growth over its North American range, but the endohydric, less drought-tolerant ***Polytrichum strictum*** (Figure 21) exhibits more constant growth throughout its range (Vitt 1990).

Figure 21. ***Polytrichum strictum*** with sporophytes. Photo by Michael Lüth, with permission.

It is possible that there is some relationship between the absence of conducting cells and the horizontal growth habit of many mosses. However, Blaikley (1932) and Bowen (1933a) disagree as to the mechanisms for external conduction, arguing about the importance of soil water, presumably more available to the pleurocarpous habit. Blaikley feels that water contributed by the soil surfaces is necessary, whereas Bowen found leaf bases had drops of water when the soil surface was dry. The methodology of tracking the water is important here, and one is encouraged to read the arguments presented by Bowen (1933a) against broad interpretations based on the use of dyes. In most cases, she argues, they would be impossible to distinguish from naturally colored tissues, and the faint stain of cortical cells may be overlooked, whereas the presence of dyes in

the central strand may be more concentrated and thus more easily discerned. Rather, Bowen argues that water, and hence dye, accumulate in the central strand, whereas their movement across the cortex is transitory only. Thus, when water appears to have reached a certain height in the stem from internal movement through the hydrom, it may in fact have arrived there from the aerial surfaces across the cortex. Using 12 plants of ***Polytrichum commune*** (Figure 9) and blocking the entry of water into the hydrome from the cut surface with wax, she was able to demonstrate rapid movement externally, up to 42 cm in one hour, reaching a maximum of 96 cm in 24 hours (Bowen 1931). When basal leaves were removed (and the wounds sealed) and the cut stems were not blocked, she demonstrated considerably less movement internally through the hydrome. Using only three plants, the greatest rise internally was only 12 cm.

It is interesting that the dependence on endohydric gametophytic conduction seems to have diminished in the evolution of bryophytes, with the creeping (pleurocarpous) taxa exhibiting less developed conducting systems. Instead, the ectohydric habit is well-developed. Yet, no pattern exists (Hébant 1977). Even the xerophytic ***Orthotrichum*** (Figure 22) lacks a central strand, although despite its acrocarpous appearance it is technically pleurocarpous and thus related to taxa that have apparently lost the central strand.

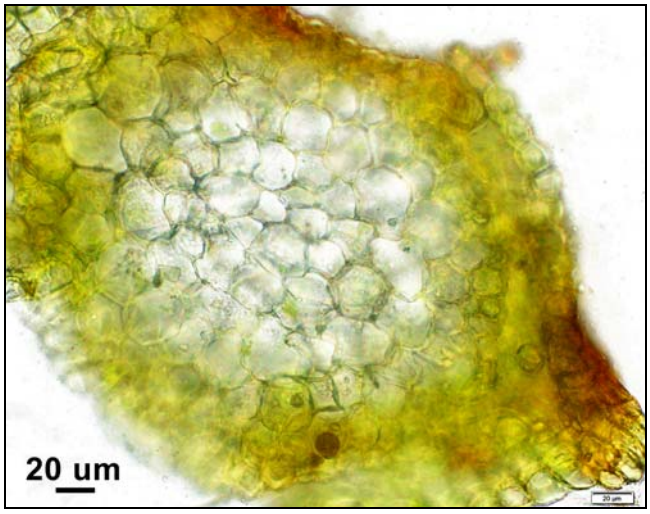

Figure 22. ***Orthotrichum pumilum*** stem cross section showing absence of central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It seems that for bryophytes, ectohydric conduction may be adaptive. Mägdefrau (1935) contends that the humidity would need to be at least 90% for the plant to succeed with internal conduction only. Gametophyte conduction is slow. Bopp and Stehle (1957) found that it required 40 hours for water to travel 10 cells in the rhizoids of ***Funaria hygrometrica*** (Figure 23)! The external pathway is much more rapid. The slowness of internal transport relative to external transport (Table 2) can easily account for the success of the external mechanisms. Furthermore, Bowen (1933a) demonstrated that the time required for movement can be more accurately measured by sensitive chemical tests that measure very small amounts of water which advance most rapidly up (or down) the plant, suggesting that external conduction is even more rapid than supposed.

To summarize, water is known to move from one bryophyte part to another by four pathways: hydroids, free spaces in cell walls, cell to cell, and externally.

Figure 23. ***Funaria hygrometrica***. Photo by Michael Lüth, with permission.

Table 2. Effectiveness of internal conduction compared to total in mosses after 24 hours in 70% relative humidity. Conduction measurements are grams water/0.2 grams dry mass; % is percent of internal compared to total rate. From Mägdefrau (1938).

	Internal Conduction	Total Conduction	%
Sphagnum recurvum	0.07	6.54	1
Drepanocladus vernicosus	0.79	22.73	3.5
Rhytidiadelphus triquetrus	0.11	1.67	6.5
Thamnobryum alopecurum	0.007	0.019	37
Plagiomnium undulatum	1.13	2.22	51
Polytrichum commune	2.24	3.32	67

Transport to Sporophyte

The seta, lacking leaves, must necessarily conduct water internally. Conduction from the gametophyte to the **sporophyte** tissue seems to be governed by several factors, as observed in ***Funaria hygrometrica*** (Figure 23) (Bopp & Stehle 1957). The sporophyte receives its water from the **haustorial foot** that is imbedded deeply into the central strand of the gametophyte.

In ***Dicranum undulatum*** (Figure 24), it appears that the embryo has a role in development of the conducting strand in the gametophyte stem, as no conducting strands were present below archegonia that had not been fertilized (Roth 1969). Hébant and Berthier (1972) made similar observations on ***Polytrichastrum alpinum*** (Figure 25). This underscores the apparent importance of the transfer of water from the gametophyte central strand to the sporophyte. There are no plasmodesmatal connections between the gametophyte and the foot of the seta (Hébant 1977). However, the **transfer cells** have extensive wall ingrowths (**labyrinth,** Figure 26) that greatly increase the surface area of the plasma membrane, thus increasing transport (Hébant 1977). In ***Funaria hygrometrica*** (Figure 23) fluorescent dyes showed that the jacket around this foot

was separated by a narrow intercellular space which became colored before the central strand (Bopp & Stehle 1957). This capillary space moved the liquid quickly to the central strand of the sporophyte. When comparing species that had no transfer cells, Bopp and Weniger (1971) found that uptake by the sporophyte was greatly reduced.

Figure 24. ***Dicranum undulatum***, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Polytrichastrum alpinum***, a moss where conducting strands seem to develop only in stems under archegonia with embryos. Photo by Michael Lüth, with permission.

Hébant (1977) describes detailed studies of a variety of mosses in which the very tip of the sporophyte foot directly penetrates the central strand of the gametophyte. At the end of the foot, an appendage of mostly necrotic cells is the only separation of the conducting cells between the two generations. Conduction in the sporophyte was increased when the calyptra was removed; the apparently non-closing stomata of the capsule may contribute to transpirational water loss.

As can be observed in ***Physcomitrium immersum*** (=*Physcomitrium cyathicarpum*), both generations have **transfer cells** at the junction, and the foot epidermal cells are rich in organelles (Lal & Chauhan 1981), especially mitochondria (Hébant 1977), suggesting there might be considerable active transport between the two generations.

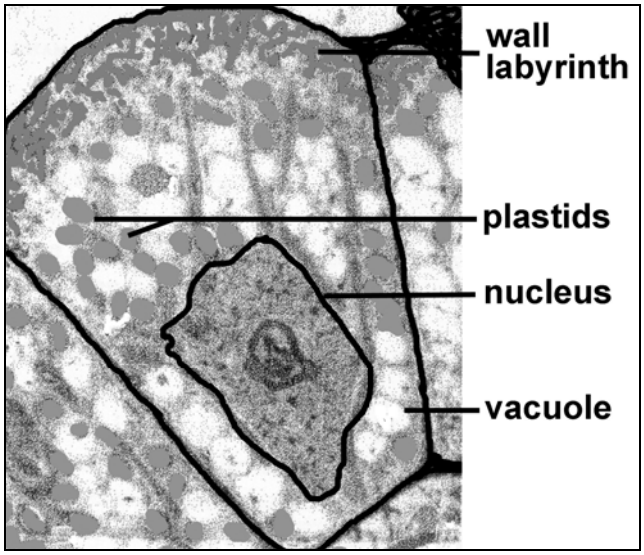

Figure 26. Transfer cell between gametophyte and sporophyte showing wall labyrinth. Computer-drawn from photo in Lal and Chauhan (1981).

Summary

We have seen that bryophytes have remarkable abilities to gain, retain, and recover from loss of water. They gain it in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Endohydric movement is accomplished either cell-by-cell or through designated elongate cells. Nutrients and water are transferred to the sporophyte through the **foot**, using special **transfer cells** with **labyrinth** walls.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself.

Literature Cited

Lal, M. and Chauhan, E. 1981. Transfer cells in the sporophyte – gametophyte junction of *Physcomitrium cyathicarpum* Mitt. Protoplasma 107: 79-83.

Bates, J. W. 2000. Mineral nutrition, substratum ecology, and pollution. In: Shaw, A. J. and Goffinet, B. (eds.). Bryophyte Biology. Cambridge University Press, Cambridge, UK, pp. 248-311.

Bayfield, N. G. 1973. Notes on water relations of *Polytrichum commune* Hedw. J. Bryol. 7: 607-617.

Beckett, R. P. 1997. Pressure-volume analysis of a range of poikilohydric plants implies the existence of negative turgor in vegetative cells. Ann. Bot. 79: 145-152.

Blaikley, N. M. 1932. Absorption and conduction of water and transpiration in *Polytrichum commune*. Ann. Bot. 46: 1-12.

Bopp, M. and Stehle, E. 1957. Zur Frage der Wasserleitung in Gametophyten und Sporophyten der Laubmoose. Z. Bot. 45: 161-174.

Bopp, M. and Weniger, H.-P. 1971. Wassertransport vom Gametophyten zum Sporophyten bei Laubmoosen. Z. Pflanzenphysiol. 64: 190-198.

Bowen, E. J. 1931. Water conduction in *Polytrichum commune*. Ann. Bot. 45: 175-200.

Bowen, E. J. 1933a. The mechanism of water conduction in the Musci considered in relation to habitat. I. Mosses growing in wet environments. Ann. Bot. 47: 401-423.

Bowen, E. J. 1933b. The mechanism of water conduction in the Musci considered in relation to habitat. II. Mosses growing in damp situations. Ann. Bot. 47: 635-661.

Bowen, E. J. 1933c. The mechanism of water conduction in the Musci considered in relation to habitat. III. Mosses growing in dry environments. Ann. Bot. 47: 889-912.

Brown, D. H. 1982. Mineral nutrition. In Smith, A. J. E. Bryophyte Ecology, Chapman & Hall, London. Pp. 383-444.

Buch, H. 1945. Über die Wasser- und Mineralstoffversorgung der Moose (Part 1). Soc. Sci. Fenn., Comment. Biol. 9(16): 1-44.

Carleton, T. J. and Dunham, K. M. M. 2003. Distillation in a boreal mossy forest floor. Can. J. Forest Res. 33: 663-671.

Castaldo Cobianchi, R. and Giordano, S. 1984. An adaptive pattern for water conduction in the ectohydric moss *Zygodon viridissimus* var. *rupestris* Hartm. J. Bryol. 13: 235-239.

Clee, D. A. 1939. The morphology and anatomy of *Pellia epiphylla* considered in relation to the mechanism of absorption and conduction of water. Ann. Bot. 3(9): 105-111.

Colbert, J. T. 1979. Spatial relations of stem hydroids to branch hydroids in four pleurocarpous mosses. Proc. Iowa Acad. Sci. 86(4): 145-148.

Csintalan, Z., Takács, Z., Proctor, M. C., Nagy, Z., and Tuba, Z. 2000. Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland. Plant Ecol. 151: 51-54.

Deloire, A., Hébant, C., and Hénon, J. M. 1979. Visualization of 'external' conduction in bryophytes by means of a fluorescent tracer. J. Hattori Bot. Lab. 46: 61-65.

During, H. J. 1992. Ecological classifications of bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). Bryophytes and Lichens in a Changing Environment, Clarendon Press, Oxford, pp. 1-31.

Goebel, K. 1915. Organographie der Pflanzen. II. Spez. Organographie 1, Bryophyten. 2. Aufl. Jena.

Hébant, C. 1970. A new look at the conducting tissues of mosses (Bryopsida): Their structure, distribution and significance. Phytomorphology 20: 390-410.

Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Lehre, Germany, 157 pp. + 80 Plates.

Hébant, C. and Berthier, J. 1972. La ramification et ses conséquences anatomiques dans la tige aérienne feuillée des Polytrichales (étude morphogénétique et histologique de quelques espéces appartenant aux genres *Polytrichum, Pogonatum* et *Dendroligotrichum*). Rev. Bryol. Lichénol. 38: 177-240.

Haas, K. 1982. The surface lipids of *Saelania* moss gametophytes: A comparison with cuticular wax of higher plants. In: Cutler D. F., Alvin, K. L., and Price, C. E. (eds.) The Plant Cuticle. Academic Press, New York. pp. 225-230.

Kawai, I. 1991. Systematic studies on the conducting tissue of the gametophyte in Musci. (18). On the relationship between the stem and the rhizome. Ann. Rept. Bot. Gard., Fac. Sci. Kanazawa Univ. 14: 17-25.

Klepper, B. 1963. Water relations of *Dicranum scoparium*. Bryologist 66: 41-54.

Lal, M. and Chauhan, E. 1981. Transfer cells in the sporophyte-gametophyte junction of *Physcomitrium cyathicarpum* Mitt. Protoplasma 107: 79-83.

Larcher, W. 1983. Physiological Plant Ecology. Trans. by M. A. Biederman-Thorson. Springer-Verlag, Berlin, 303 pp.

Ligrone, R. and Duckett, J. G. 1998. The leafy stems of *Sphagnum* (Bryophyta) contain highly differentiated polarized cells with axial arrays of endoplasmic microtubules. New Phytol. 140: 567-579.

Lorch, W. 1931. Anatomie der Laubmoose. In: Linsbauer, K. (ed.). Handbuch der Pflanzenanatomie VII/I. Gebrüder Borntrager, Berlin, 358 pp.

Mägdefrau, K. 1935. Untersuchungen über die Wasserversorgung des Gametophyten und Sporophyten der Laubmoose. Zeitschr. Bot. 29: 337-375.

Mägdefrau, K. 1938. Reviews of recent research. 2. Der Wasserhaushalt der Moose. Ann. Bryol. 10: 141-150.

Maier-Maercker, U. 1982b. Accumulation of 86Rb, 43K and heavy metal ions in the annulus of the moss *Mnium cuspidatum* (L.) Leysser: A parallel to guard cell ion uptake. Zeits. Pflanzenphysiol. 108: 107-111.

Mizushima, U. 1980. Water relations in *Entodon rubicundis* (Mitt.) Jaeg. Proc. Bryol. Soc. Japan 2(9): 124-126.

Nobel, P. S. 1977. Internal leaf area and cellular CO_2 resistance: Photosynthetic implications of variations with growth conditions and plant species. Physiol. Plant. 40: 137-144.

Oliver, M. J. and Bewley, J. D. 1984. Plant desiccation and protein synthesis. IV. RNA synthesis, stability, and recruitment of RNA into protein synthesis during desiccation and rehydration of the desiccation-tolerant moss, *Tortula ruralis*. Plant Physiol. 74: 21-25.

Proctor, M. C. F. 1979a. Structure and eco-physiological adaptations in bryophytes. In Clarke, G. C. S. and Duckett, J. G. (eds.): Bryophyte Systematics. Systematic Association special volume 14. Academic Press, London, pp. 479-509.

Proctor, M. C. F. 1979b. Surface wax on the leaves of some mosses. J. Bryol. 10: 531-538.

Proctor, M. C. F. 1980. Diffusion resistances in bryophytes. In: Ford, E. D. and Grace, J. (eds.). Plants and Their Atmospheric Environment. Symp. Brit. Ecol. Soc., pp. 219-229.

Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman and Hall, London, pp. 333-381.

Proctor, M. C. F. 1984. Structure and ecological adaptation. In: Dyer, A. F. and Duckett, J. G. (eds.). The Experimental Biology of Bryophytes. Academic Press, London, pp. 9-37.

Richardson, D. H. S. 1981. The Biology of Mosses. John Wiley & Sons, Inc., N. Y., 220 pp.

Roth, D. 1969. Embryo und Embryotheca bei den Laubmoosen. Eine histogenetische und morphologische Untersuchung. Biblio. Bot. 129: 1-49.

Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140: 677-684.

Slatyer, R. O. 1967. Plant-Water Relationships. Academic Press, London.

Trachtenberg, S. and Zamski, E. 1979. The apoplastic conduction of water in *Polytrichum juniperinum* Willd. gametophytes. New Phytol. 83: 49-52.

Wijk, R. Van der. 1932. Morphologie und Anatomie der Musci. In: Verdoorn, F. (ed.). Manual of Bryology, Martinus Nijhoff, The Hague.

Vitt, D. H. 1990. Growth and production dynamics of boreal mosses over climatic chemical and topographic gradients. Bot. J. Linn. Soc. 104: 35-59.

Zacherl, H. 1956. Physiologische und Okologische Untersuchungen über die innere Wasserleitung bei Laubmoosen. Z. Bot. 44: 409-436.

Zamski, E. and Trachtenberg, S. 1976. Water movement through hydroids of a moss gametophyte. Israel J. Bot. 25: 168-173.

CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

TABLE OF CONTENTS

Water Strategies 7-3-2
Water Cycle Role in Ecosystem 7-3-7
Structural Adaptations 7-3-7
Thallose Liverworts 7-3-8
Scales 7-3-8
Ballooning of Epidermis 7-3-9
Rhizoids 7-3-9
Fungal Partners 7-3-13
Main Thallus Structure 7-3-13
Spongy Thallus 7-3-14
Cuticle 7-3-14
Pores 7-3-15
Archegoniophores and Antheridiophores 7-3-17
Dormancy 7-3-19
Mosses and Leafy Liverworts 7-3-19
Growth Form 7-3-21
Stems and Branches 7-3-22
Central Strand 7-3-25
Waxes 7-3-26
Rhizoids and Tomentum 7-3-26
Mucilage 7-3-29
Capillary Spaces 7-3-30
Fungal Partners 7-3-32
Protonema 7-3-33
Leafy Liverwort Gemmae 7-3-33
Sporophyte 7-3-33
Calyptra Protection 7-3-34
Cuticle 7-3-35
Guard Cells and Stomata 7-3-40
Summary 7-3-45
Acknowledgments 7-3-46
Literature Cited 7-3-46

CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

Figure 1. ***Tortula muralis*** with water drops collected on the leaf awns and setae. Note their collection around the young capsules. Photo courtesy of Peggy Edwards.

Water Strategies

Water strategies in bryophytes have been approached in a variety of ways, from splashing gemmae (Brodie 1951) to uptake (Proctor 1981; Rice & Schneider 2004; Rice 2012; Jonas & Dolan 2012; Sand-Jensen & Hammer 2012) to transport (Hébant 1977; Mulder *et al*. 2001; Proctor & Tuba 2002; Pressel 2006; Rice 2012) to moving nutrients (Buch 1945, 1947; Proctor 1981) to retention (Kennedy 1993; Mulder *et al*. 2001; Rixen & Mulder 2005).

Mosses often appear to be completely dead, only to be revived by water. Angela Newton (pers. comm., Bryonet) reported that epiphytic mosses in the lowland tropical rainforests, where mosses may appear dead after severe desiccation, recover quickly with actively growing apical and axillary buds on completely dried out plants and even on plants scorched by fire (see Figure 2)! Leaf and stem tissues from xerophytic mosses can regenerate after as many as 19 years of desiccation (Table 1); some spores remain viable after 70 years (Malta 1921). As surmised by Oliver *et al*. (2005), **desiccation tolerance** appears to be a primitive trait that permitted plants to invade land. **Desiccation tolerance** (**DT**) is the ability of an organism or structure to tolerate and survive after equilibrating to a relative humidity (RH) of ≤50% (Alpert & Oliver 2002; Koster *et al*. 2010). An understanding of this tolerance in modern bryophytes is fundamental to a general understanding of desiccation tolerance.

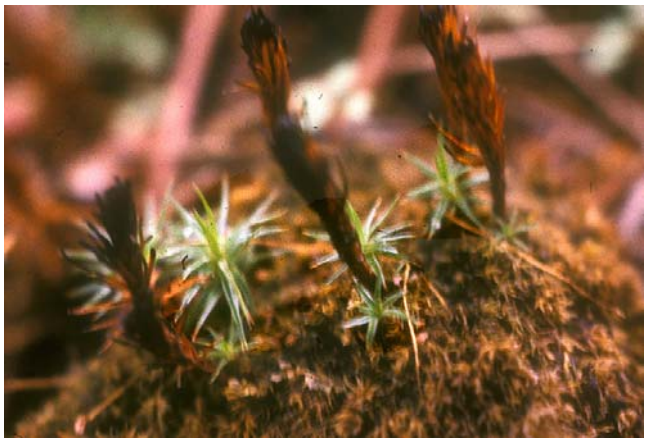

Figure 2. ***Polytrichum*** showing fresh, green growth one week after a forest fire that scorched adjacent plants in Baraga, Michigan, USA. Photo by Janice Glime.

Table 1. Records of revival after extended periods in a herbarium (Alpert 1982, *Volk 1984, +Glime pers. obs.).

Anoectangium compactum	19 years
Dicranoweisia cirrata	9 years
Riccia canescens	*7 years
Grimmia elatior	5 years
Oxymitra	*4 years
Anomodon longifolius	2 years
Bryum argenteum	2 years
Orthotrichum rupestre	2 years
Grimmia muehlenbeckii	18 months
Andreaea rothii	13 months
Racomitrium lanuginosum	11 months
Syntrichia ruralis	8 months
Fontinalis flaccida	+3 months

Most people who are not very familiar with bryophyte physiology consider them to be plants that require damp or wet habitats. But compared to **tracheophytes** (non-bryophytes; plants with lignified vascular tissue), bryophytes are the ones adapted to drying conditions (Vitt *et al*. 2014). Even in bryophytes that seem to lack physiological desiccation tolerance, morphological or life history adaptations permit them to survive periodic drought.

In fact, of the known 18,000 species of bryophytes (Shaw & Goffinet 2000), 210 have been documented as desiccation tolerant (Wood 2007), but most have never been tested. Among seed plants, fewer than 1% of those tested are desiccation tolerant (Proctor & Pence 2002). Even the aquatic moss ***Fontinalis*** has at least some desiccation-tolerant species (Glime 1971). For example, ***Fontinalis flaccida*** survived and grew after three months of drying on a herbarium sheet (pers. obs.). If one considers the types of microhabitats bryophytes occupy, and lack in most species of any kind of water storage organ, we should expect that most have at least some degree of desiccation tolerance. This notion is further supported by the high survival rate of bryophytes despite a high surface-to-volume ratio that facilitates rapid drying (Proctor *et al.* 2007).

Proctor and Tuba (2002) considered there to be two contrasting strategies for land plants to deal with the irregular supply of water they faced on land and that these relate closely to the matter of scale. Tracheophytes use internal transport to carry water from the soil to the distant canopy (**homoiohydry**). Bryophytes (and some tracheophytes), on the other hand, depend on desiccation tolerance, becoming dormant when desiccated. Hence, their cells are either **turgid** (swollen) or desiccated. But desiccation tolerance requires a whole series of adaptations to permit the cell to regain its original state. This strategy is particularly beneficial on hard substrates such as rocks and on dry soils in seasonally dry climates. Thus, among tracheophytes, this strategy is most common in warm semiarid climates, whereas in mosses the strategy occurs from polar to tropical regions (Proctor & Tuba 2002; Lakatos 2011). The time scale also differs, with tracheophytes requiring one to several days to resume activity whereas bryophytes (and lichens) typically require an hour or less (Proctor & Tuba 2002).

Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] desiccation tolerance exist among plants (Stark *et al*. 2013) and these will be discussed in Chapter 7-6 of this volume.

Cellular structure remains intact in desiccation, but upon rapid uptake of water it can be disrupted. However, in bryophytes the cellular integrity returns rapidly. Photosynthetic activity recovers quickly, perhaps due to protection of the chlorophyll (Tuba 1984; 1985). During desiccation, there seems to be no gene activity, but gene expression occurs rapidly following rehydration. Among these activities is the production of a number of proteins called **rehydrins**. These seem to be involved in stabilizing and reconstituting membranes that have been damaged by dehydration. Oliver *et al*. (2005) suggest that vegetative desiccation tolerance, at least in bryophytes, has changed little from early land invaders and may be using a mechanism that was first used in spores.

Even though many bryophytes tolerate high degrees of desiccation (Dilks & Proctor 1974; Nörr 1974; Dhindsa & Bewley 1976), **water content** and availability are important for potential accumulation of photosynthates (Alpert 1979). Patidar (1988) found that in ***Asterella angusta*** the moisture content is the most important determinant of **thallus** (flattened, nonvascular plant body) size. In ***Plagiochasma appendiculatum*** (Figure 3), optimum growth occurs at 60% moisture, whereas branching and growth are able to occur from 10-100% moisture (Vishvakarma & Kaul 1988)! ***Reboulia hemisphaerica*** (Figure 4), on the other hand, requires 70-80% moisture for optimum growth, with growth and branching occurring from 40 to 90%. In other words, no matter how desiccation tolerant a plant might be, it requires water to grow. Representative water contents of bryophyte plants from a wide range of field habitats in the temperate zone, Great Britain, are given in Table 2.

Figure 3. ***Plagiochasma appendiculatum***, a liverwort with both branching and growth throughout the range of 10-100% moisture. Photo by Michael Lüth, with permission.

Figure 4. ***Reboulia hemisphaerica***, a liverwort in which growth and branching occur in the range of 40-90% moisture. Photo by Jan-Peter Frahm, with permission.

Table 2. Percent water content (compared to dry mass) of bryophytes at full turgor, not including free external water. Values represent means of two measurements. Table based on Dilks and Proctor (1979); those marked with * from Skre *et al*. (1983) include new growth and 1-year-old growth; those with + from Proctor (2000).

species	water content, % dry mass
Mosses	
*Sphagnum subsecundum**	1225
Pilotrichella ampullacea+	>1200
Hookeria lucens	516
*Pleurozium schreberi**	485-625
*Hylocomium splendens**	485-545
Brachythecium rutabulum	249
Syntrichia intermedia	233
Homalothecium sericeum	223
Pseudoscleropodium purum	207
Thuidium tamariscinum	203
Dicranum majus	202
Leptodon smithii	187
Rhytidiadelphus loreus	165
Pleurochaete squarrosa	165
Neckera complanata	162
Racomitrium lanuginosum	142
Anomodon viticulosus	141
*Polytrichum commune**	95-125
Liverworts	
Pellia epiphylla	1180
Conocephalum conicum	871
Porella platyphylla	230
Plagiochila spinulosa	222
Bazzania trilobata	210

Mosses grown in fully hydrated conditions afforded by saturated air enjoy optimal growth and development (Davy 1927). They exhibit more rapid development, more stem branching, more numerous rhizoids, smaller leaves, and smaller and fewer cells with larger chloroplasts than mosses existing at less than full saturation. Even at the scale of a single boulder, bryophytes distribute themselves according to their ability to achieve photosynthetic gain. When examining bryophytes that occupied various microsites on exposed granitic boulders, Alpert and Oechel (1987) found that those species that occurred in microsites with lower water availability were able to attain maximum net photosynthetic gain at a lower water content and to recover better from prolonged desiccation than those taxa in less **xeric** (dry) microsites. Alpert (1985, 2000) supports the hypothesis that the reason even **xerophytic** mosses (those adapted to dry habitats) are limited in their ecological distribution is that they often are unable to maintain positive carbon balance during repeated cycles of wetting and drying. Alpert and Oechel (1985) demonstrated this with ***Grimmia laevigata*** (Figure 5-Figure 6), a desiccation-tolerant plant that was unable to maintain this balance under a natural, highly xeric regime of wetting and drying in certain microhabitats on exposed granitic boulders in California chaparral. Thus, there is an "inherent trade-off between desiccation tolerance and growth rate."

Figure 5. ***Grimmia laevigata***, a poikilohydric moss, in its dry state. Photo by Michael Lüth, with permission.

Figure 6. ***Grimmia laevigata***, a poikilohydric moss, in its wet state. Photo by Michael Lüth, with permission.

Water content in a bryophyte ranges widely throughout the year. For example, Klepper (1963) measured 23.8-258% in ***Dicranum scoparium*** (Figure 7), Romose (1940) 10-950% in ***Homalothecium sericeum*** (Figure 8), Morton (1977) 19-214% in ***Pseudoscleropodium purum*** (Figure 9), and 58-307% in ***Dicranum bonjeanii*** (Figure 10). Whereas many mosses benefit from high water content, too much water is not good for photosynthesis. Water on the surface blocks CO_2, and most likely high internal water content also interferes with physiological processes (Proctor 2000). Dilks and Proctor (1979) found optima as low as 200% water content and as high as 1500% among the same bryophytes shown in Table 2. Respiration seems to peak around 200% for most of these taxa.

Figure 7. ***Dicranum scoparium***, a moss with measured water content ranging 23.8-258%. Photo by Janice Glime.

Figure 8. ***Homalothecium sericeum***, a moss with measured water content ranging 19-214%. Photo by David Holyoak, with permission.

Figure 9. ***Pseudoscleropodium purum***, a moss with measured water content ranging 19-214%. Photo by Michael Lüth, with permission.

Richardson (1981) divides mosses into three water strategies by habitat: **aquatic**, **mesophytic** (living in continually moist habitats), and **poikilohydric** (organism dries as its habitat dries and resumes normal metabolic activity after rehydration; Figure 6). Unlike most other plants, water content of predominantly poikilohydric bryophyte species is highly related to environmental conditions and weakly regulated by their internal and morphological structures. This strategy permits them to colonize such xeric environments as boulders and tree trunks. In these environments, mosses enjoy release from competition by higher plants, but must still survive the low light intensity created by the trees above.

Figure 10. ***Dicranum bonjeanii***, a moss with measured water content ranging 58-307%. Photo by Michael Lüth, with permission.

Some bryophytes do appear to be able to survive in absence of precipitation. In caves in Poland, only 18.1% of the species occurred in very wet places or where there was dripping water, whereas in places that were continuously dry(!), 25% occurred (Jedrzejko & Ziober 1992). Certainly in those dry places atmospheric humidity must have provided the needed water for these very **hygroscopic** (readily absorbing water from air), **ectohydric** (relying mainly on water transport along external surface of plant by capillarity) bryophytes. Shaun Russell (pers. comm.) found that in montane areas of Africa with virtually no rainfall, fog collected on bryophyte surfaces, providing sufficient water for them to survive. A similar phenomenon occurs in geothermal areas (Figure 11).

Figure 11. ***Campylopus holomitrius*** with water droplets captured from the "steam" emitted by geothermal vents in New Zealand. Photo by Janice Glime.

The drought-tolerant ***Pseudocrossidium crinitum*** (=*Barbula aurea*; Figure 12) seems to have compensated for its low water availability by having relatively low levels of light compensation and saturation responses for photosynthesis (Rundel & Lange 1980). Such low levels would permit the moss to carry out photosynthesis early in the morning when dew is available and before high evaporation stress occurs. These aerial sources of water are of little use to tracheophytes that must take water in by their roots, not their leaves.

Figure 12. ***Pseudocrossidium crinitum***, a xerophyte with low light compensation and saturation levels. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

As one would expect, degree of drought tolerance is generally greatest in plants from dry habitats (Clausen 1952, 1964; Johnson & Kokila 1970; Dilks & Proctor 1974). Seki and Yamaguchi (1985) suggest that on some islands with strong summer winds, Shannon diversity decreases as saturation deficits increase. Richardson (1981) claims that aquatic mosses and those that grow in humid forests are damaged quickly by drought. But even such high humidity plants as ***Hookeria lucens*** (Figure 13) are able to survive desiccation for days (Horst Tremp, Bryonet).

Figure 13. ***Hookeria lucens***, a drought-intolerant moss. Photo by Michael Lüth, with permission.

Glime (1971) found that two aquatic mosses (***Fontinalis*** spp.; Figure 14) were able to survive on the stream bank out of water (Figure 15) for up to one year and still grow when rehydrated. However, those dried in the laboratory were apparently dead after only 55 hours, perhaps due to rapid drying. Steere (1976) found that ***F. squamosa*** (Figure 16) from Alaska could not survive a week of air drying. One reason for apparent differences here is that it is difficult to determine when a moss is dead, and even though all leaves may be dead, the stem may still harbor life. ***Fontinalis*** is subject to annual emergence when stream level drops (Figure 14), and perhaps slow drying on the stream bank permitted it to become dormant and to preserve sufficient energy to repair its membranes upon rehydration. The rapid drying of a laboratory, with unnaturally low humidity and no acclimation period, may have prevented the necessary physiological changes that could permit it to survive. It is well known that it takes longer for the cellular physiology to return to normal in a rapidly dried bryophyte than in a slowly dried one (Oliver & Bewley 1984).

Figure 14. ***Fontinalis dalecarlica*** and ***F. novae-angliae*** above water, in Fox Run, NH, USA. When these mosses were placed away from the stream bed for up to one year, at least some of them survived from all re-submersion dates (Glime & Carr 1974). Photo by Janice Glime.

Figure 15. ***Fontinalis antipyretica*** in dry stream. Photo by Janice Glime.

Figure 16. ***Fontinalis squamosa*** on rock above water near Swallow Falls, Wales. Photo by Janice Glime

A similar pattern of submersion and desiccation is endured by ***Hydropogon fontinaloides*** in the Amazon basin (Mägdefrau 1973). It hangs from trees during the dry season, but during the wet season it floats in water. The behavior of ***Cratoneuron filicinum*** (mistakenly published as *Hygrohypnum luridum*; Figure 17), typically a stream margin species, may explain the lab results. This moss was unable to synthesize protein when rehydrated after it was dried quickly over silica gel for one hour (Bewley 1974). However, it was able to tolerate drying down to 33% of its fresh mass when dried slowly, and slow drying for 5 hours to 66% of its fresh mass had no detrimental effects on protein synthesis.

Figure 17. ***Cratoneuron filicinum***, a moss that is unable to synthesize protein when rehydrated if it dries too quickly. Photo by Teplov through Arctoa, with permission.

Just what endows bryophytes with the ability to inhabit arid microsites that are totally inhospitable for tracheophytes? As you can see from the foregoing examples, we can divide these adaptations into anatomical/structural, growth/life form, and physiological adaptations.

Life cycle adaptations, a major means for an immobile organism to cope with changing weather and seasons, have been addressed in Chapter 4-6. Schofield (1981) points out that spore germination patterns, protonemal structure, life span, and methods of propagation are all related to the habitat characteristics. Water availability is important to all of these aspects. Multicellular spores are more common in habitats where the spores are subject to desiccation. Protonematal specialization is common in deeply shaded habitats, whereas in mesic habitats the protonemal cells are elongate, *i.e.*, having typical protonematal structure. In the leafy **gametophore** (upright leafy plant), characters such as leaf shape, leaf arrangement and orientation, leaf anatomy, stem cortical cells, hydroids, leptoids, branch arrangement, presence of rhizoids, and presence of paraphyllia all affect water movement. Such small features as surface ornamentation of leaves, stems, and rhizoids affect water absorption and retention and influence habitat specificity.

Water Cycle Role in Ecosystem

In areas where bryophytes dominate the forest floor, their role in the water cycle can be extraordinary. This is especially true where permafrost prevails (Henry Santeford, pers. comm.). Bryophytes hold melt water until they become saturated. At that point in time, all new melt water is suddenly released and can cause flooding. It is important in some areas to be able to predict this flooding regime for the safety of both animals and humans. Hence, we need to understand both holding capacity and evaporation rates of water from the bryophytes.

Penman (1948) helps us to understand evaporation as it might apply to bryophytes. Although he compared evaporation from bare soil, grass, and open water, the principles apply. He suggests that we need to combine two theoretical approaches to evaporation, an aerodynamic basin in which evaporation is due to turbulent transport of vapor by eddy diffusion, and an energy basis in which evaporation is a way of degrading incoming radiation. This approach eliminates the problem of measuring surface temperature and overcomes the problem of estimating effects as if one is measuring evaporation from a lake surface. Using this method, supported by empirical data, indicates that evaporation from grass follows a seasonal cycle relative to that evaporating from open water, a phenomenon Penman attributes to the change in photoperiod.

In other circumstances, bryophytes may prevent the underlying roots from getting water (Beth Scafone, unpubl. data). If there is a quick rain shower, bryophytes act as sponges, trapping the water before it reaches the soil. On the other hand, bryophytes can reduce evaporation of water from the soil following heavy rain, thus permitting the roots to grow for longer periods of time.

Structural Adaptations

When I moved to the Upper Peninsula of Michigan, I was struck by the fact that only red oaks were able to live here. A simple difference in one structure made their survival possible in a cold region with long winters – narrow vessels. Large vessels in the other North American species cavitate and the water is unable to reconnect on an appropriate time schedule that permits the oaks to complete their life cycle and gain sufficient energy to continue the establishment of the species.

Many studies have demonstrated the importance of anatomy in determining the mechanical properties of plant tissues, including bryophytes (Hébant 1977; Rossi *et al*. 1998; Niklas *et al*. 2006; Frenzke *et al*. 2011; Atala & Alfaro 2012; Vincent 2012). Getting water and nutrients into and out of a plant is size dependent. Adaptations vary even within a species due to its plasticity in responding to the environment (Sarafis 1971; Buryová & Shaw 2005). As discussed by Raven and Handley (1987), for plankton organisms, any size above ~50 µm diameter restricts the growth rate because of the greater restriction of uptake by the boundary layer. Thus, for macroscopic aquatic photosynthetic organisms, even favorable velocity of water and plant morphology cannot reduce the boundary layer restrictions on nutrient uptake enough to compensate for the decrease in uptake rate. Movement of nutrients within the plant involves **cyclosis** (cytoplasmic streaming) in algae, phloem and xylem in tracheophytes, and in bryophytes it often involves both cyclosis and transport through leptoids and hydroids.

Raven and Handley (1987) consider that the energy cost for transporting nutrients would be higher for those organisms using cyclosis than for those using vascular tissue. They also consider that there is a penalty for height in tracheophytes, causing reduced specific growth rate under both resource-saturated and resource-limited conditions. Coupled with this penalty is reduced resource use efficiency with increased plant height. The reason for these penalties is the need for greater supporting tissue and a greater percentage of the tissue dedicated to vascular tissue. But there is also some compensation. Taller plants can capture more light energy and reach more nutrients and water in the soil. Smaller plants, on the other hand, have a potentially higher specific growth rate under these same resource-limited or resource-saturated conditions. The lack of need for supporting structures, requiring breadth, permits smaller plants such as bryophytes to have all or nearly all of their tissues as photosynthetic tissues. Raven and Handley left us with the challenge to discover the differences in transport needs and solutions resulting from these different morphologies.

In the desert moss ***Syntrichia caninervis*** (Figure 18), conservation of moisture is paramount, surpassed only by the need for rapid uptake. It can therefore serve as a model for adaptations against desiccation. Its growth form is tufted and its leaves are folded upward and twisted around the stem when dry (Zheng *et al*. 2010). The leaf cells are endowed on both the upper and lower surfaces with C-shaped papillae that may have a role in deflecting sunlight to protect the DNA and chlorophyll during dry periods or to reduce the temperature. The leaf costa extends beyond the leaf to form an awn that has forked teeth and is able to capture moisture from the atmosphere. The protonemal cells are small and have thick walls; their cytoplasm is highly concentrated with only a small vacuole.

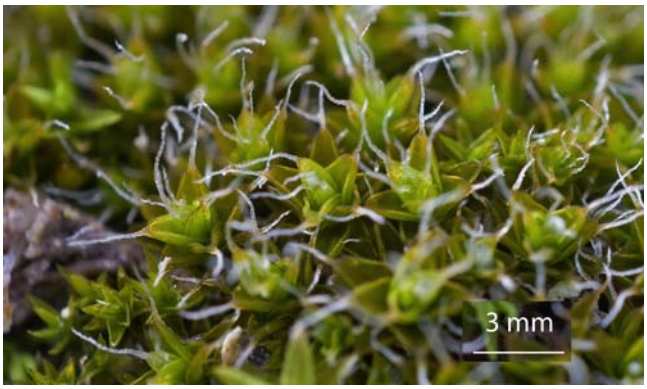

Figure 18. ***Syntrichia caninervis***, a desert moss that increases its wax content as it ages. Note the awns that can trap atmospheric moisture from fog. Photo from Proyecto Musgo, through Creative Commons.

Thallose Liverworts

The structure of most thallose liverworts is so different from that of mosses or leafy liverworts that their water relations warrant separate consideration. They are adapted for predominantly ventral uptake. Thallose liverworts like ***Conocephalum conicum*** (Figure 19) and ***Cyathodium cavernarum*** (Figure 20) use ventral appendages (**scales;** Figure 19) to provide capillary spaces that conduct water externally on the underside of the thallus. Marchantialian species use specialized capillary systems on the ventral surface of the thallus to conduct water in either direction. Cell walls of the scales contain **tannins** (McConaha 1939), perhaps acting as an antibiotic.

Scales

Exposed surfaces of scales and thallus are often reddish-purple due to the flavonoid pigment **phlobaphene**, formed by oxidation of tannic compounds (McConaha 1939), but the role of phlobaphene is not clear. It is possibly a defense against would-be toxins from tannic compounds that contact the ventral surface. (There is evidence that tannins are toxic to bryophytes, not within their cell walls, but when they are able to act on cell constituents.) Since all these ventral surfaces are wettable, these cells are more susceptible to damage by such toxins.

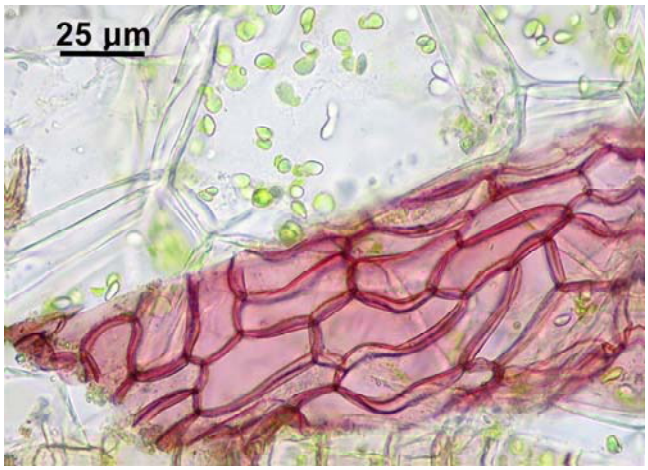

Figure 19. ***Conocephalum conicum*** showing ventral scale (purple) that provides capillary spaces for external water movement. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

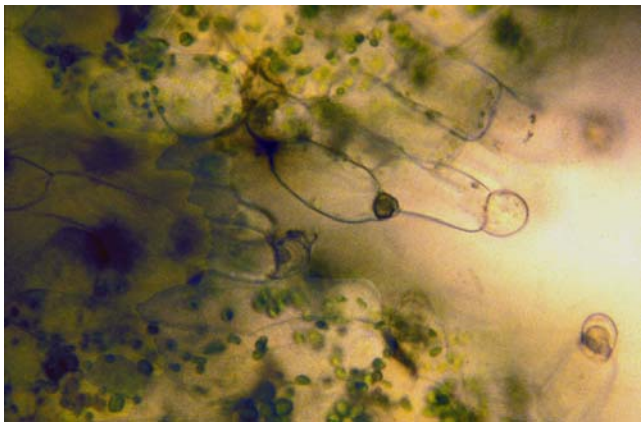

Figure 20. Scales of ***Cyathodium cavernarum***. Photo courtesy of Noris Salazar Allen.

Kürschner (2004) surmised that the anthocyanin pigments in ventral scales protected the ventral surface from the sun when the thallus was rolled up, as it typically does in many species of ***Riccia***. Furthermore, even hyaline scales of ***Riccia*** and ***Oxymitra*** (Figure 21) can reduce desiccation. Some species, especially of ***Riccia***, sink into the soil surface as the soil dries, reappearing only after precipitation or heavy dew.

Figure 21. ***Oxymitra incrassata*** showing ventral hyaline scales at the margins. Photo by Michael Lüth, with permission.

This high degree of wettability provides a greater possibility for water entry in thallose forms. For example, in ***Marchantia*** (Figure 22-Figure 23), water is conducted along the midrib as well as in interstitial spaces between the blade and scales, distributing water throughout the surface of the thallus. Water movement in ***Marchantia*** is relatively slow, at 0.4 mm per sec, improving slightly in ***Lunularia*** (Figure 44-Figure 45) and ***Reboulia*** (Figure 4), to approximately 0.5 mm per sec, despite their less highly developed capillary systems. However, McConaha (1939) found that movement from base to apex in ***Conocephalum conicum*** (Figure 24) generally takes only about 20-30 seconds, roughly 1 mm per sec. Despite its slowness, McConaha found this external movement to be much faster than would be possible by internal conduction.

Figure 22. ***Marchantia polymorpha*** with gemmae cups located on the midrib. Photo by Walter Obermayer., with permission.

Ballooning of Epidermis

In some species of ***Riccia*** the epidermis is balloon-like and may contribute to protection from desiccation (Kürschner 2004). However, I wonder if those cells don't provide a greater role in focussing the light into the thallus to the chlorophyllous cells when the thallus is hydrated. Kürschner suggested that the chimney-like, hyaline air chambers of ***Exormotheca*** (Figure 25-Figure 27) may also have a function in protecting the underlying tissue during dehydration.

Figure 23. ***Marchantia polymorpha*** ventral surface showing blackish midrib (**arrow**) and white scales and rhizoids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 24. ***Conocephalum conicum***, where water travels from base to apex in about 20-30 seconds. Photo by Janice Glime.

Figure 25. ***Exormotheca pustulosa*** showing ballooning of epidermal cells. Photo by Jonathan Sleath, with permission.

Figure 26. ***Exormotheca welwitschii*** showing ballooning of epidermal cells. Photo by Michael Lüth, with permission.

Figure 27. ***Exormotheca*** thallus section showing columns of photosynthetic tissue and ballooning surface. Photo by Wilhelm Barthlott, with permission.

Rhizoids

Ventral structures seem to be important in this group. In marchantialian liverworts, two types of rhizoids (Figure 29-Figure 28) provide somewhat different functions. The smooth-walled rhizoids (Figure 28) are alive (Duckett & Ligrone 2003) and emerge from beneath the ventral scales (Figure 30), providing contact with the substrate, whereas the **tuberculate** (pegged) rhizoids (Figure 28) are dead (Duckett & Ligrone 2003) and form a capillary system parallel to the thallus beneath each scale (McConaha 1941). The pegged rhizoids begin growth at right angles to the thallus but change their orientation to follow that of the scales. The pegs, extending into the pegged rhizoid cell, prevent the collapse of the cell when dehydrated, thus maintaining its capillary role (Duckett & Ligrone 2003). When the **archegoniophore** (stalk supporting female reproductive organs) forms, the pegged rhizoids are wrapped within the archegoniophore by the folded thallus (Figure 31) and function in internal water conduction (Duckett & Ligrone 2003). The presence of the pegs also prevents the collapse of this stalk when the thalli dehydrate (Duckett & Ligrone 2003). These rhizoids have an outer layer of pectic material (like apples).

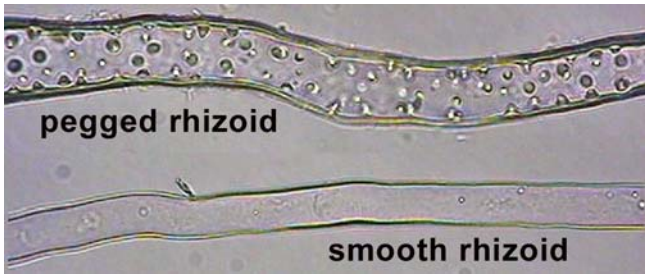

Figure 28. Pegged and smooth rhizoids of ***Conocephalum conicum***. Photo by Paul Davison, with permission.

Figure 29. ***Riccia*** sp. with rhizoids on ventral side. Photo by Bernd Haynold, through Creative Commons.

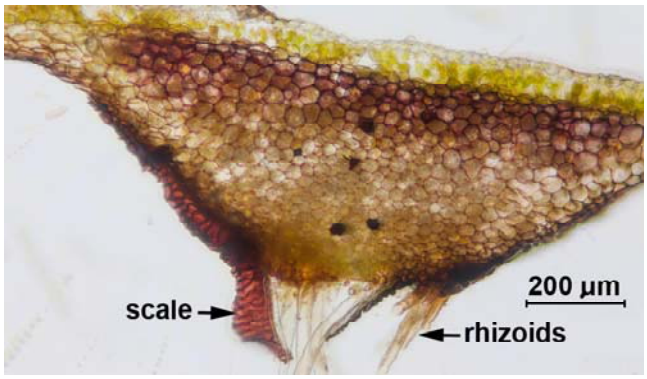

Figure 30. ***Preissia quadrata*** thallus cross section showing position of scale and rhizoids. Photo by Kristian Peters, with permission.

Figure 31. ***Marchantia polymorpha*** archegoniophore showing white rhizoids that are incompletely enclosed by the stalk of the archegoniophore. Photo by George Shepherd, through Creative Commons.

Previously treated mostly as a taxonomic anomaly, it appears that these two types of rhizoids have distinctly different functions (Duckett *et al*. 2013). The smooth rhizoids are alive, functioning in nutrition, anchorage, and as entry locations and conduits for fungal symbionts. Their role for fungal entry does indeed require that these rhizoids be alive. The pegged rhizoids, on the other hand, are dead at maturity, a condition first noted by Kamerling (1897), and function as water conduits through these empty tubes. Kny (1890) was the first to suggest that pegs prevent the rhizoid walls from collapse with water loss. Duckett *et al*. (2013), however, were the first to test this hypothesis. The pegs, along with elasticity, seem to provide the ability of the rhizoids to maintain their functional integrity by preventing their collapse when they are dry. This ability is essential to their function in conduction, a role demonstrated by Bowen (1935) and others (McConaha 1939, 1941), who used dyes to show conduction by capillarity and transpiration. The famous German morphologist Goebel (1905) observed that it is the liverworts with high transpiration rates that also have the most highly developed pegged rhizoids. This is in contrast with those of **hygrophilous** (water-loving) taxa such as ***Dumortiera*** (Figure 32-Figure 33) and ***Cyathodium*** (Figure 34).

Figure 32. ***Dumortiera hirsuta***, a hygrophilous species showing fringe of hairs on thallus and archegonial heads, but lacking the pegged rhizoids and scales of the dry habitat species. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Dumortiera hirsuta*** thallus showing rhizoids on the ventral surface. Photo by Chris Lobban, with permission.

Among the leafy liverworts, thallose liverworts, and ferns, living rhizoids die and collapse upon dehydration, an irreversible response (Pressel 2007). Duckett *et al*. (2013) concluded that smooth rhizoids of liverworts grow at the apex, a character they share with root hairs, fungal hyphae, and moss protonemata. Furthermore, the smooth rhizoids exhibit considerable endoreduplication of Golgi bodies similar to that in moss caulonemata. They reach lengths that commonly are greater than 20 mm, sometimes reaching 30 mm in ***Marchantia polymorpha*** (Figure 23), making them the longest cells in liverworts. Duckett and coworkers suggest that this combination of characters may explain their inability to regenerate when damaged (Pressel *et al.* 2008a; Duckett *et al*. 2013).

Figure 34. ***Cyathodium tuberosum***, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Jan-Peter Frahm, with permission.

On the other hand, rhizoids of mosses (and protonemata) can recover from desiccation except at the apical cell (Pressel 2007; Rowntree *et al.* 2007; Pressel *et al.* 2008b). The pegged rhizoids furthermore are devoid of air bubbles when desiccated, a further indication that they are highly resistant to **cavitation** (formation of a space; collapse of cells), as are the hydroids of mosses (Ligrone *et al*. 2000).

Duckett *et al*. (2013) identified pegged rhizoids in 26 species of thallose liverworts and absence in 5. They compared the diameters of the smooth and pegged rhizoids and measured the time required for dyes to reach the archegonial heads in the taxa compared to time required in several mosses. The rates ranged 30-150 mm h^{-1} in the thallose liverworts, 28-14 mm h^{-1} in mosses, and 127-141 mm h^{-1} in ferns.

Duckett *et al*. (2013) point out that these pegged rhizoids fulfill the three criteria for conduction defined by Raven (1993): dead at maturity, specialized walls, preferential conduction of water. Duckett and coworkers added a fourth criterion, the ability to maintain functional integrity through periods of dehydration, as in moss hydroids (Ligrone *et al*. 2000). This maintenance of functional integrity becomes a problem, because unlike trees and stems, there is no adjacent cell to help in rehydration.

Xerophytic liverworts such as ***Riccia*** (Figure 35), ***Reboulia*** (Figure 4), ***Targionia*** (Figure 36), ***Asterella*** (Figure 37), and ***Lunularia*** (Figure 44-Figure 45) have both **tuberculate** (pegged) and smooth rhizoids, scale

leaves, and well-defined assimilatory and storage zones, whereas moisture-loving ***Dumortiera*** (Figure 32), ***Cyathodium*** (Figure 34), ***Pallavicinia*** (Figure 38) (Daniels 1998), ***Monoclea*** (Figure 39), ***Neohodgsonia*** (Figure 40), and some aquatic ***Riccia*** species (Figure 41-Figure 42) (Duckett & Ligrone 2003) lack these complex structures. Even in ***Marchantia*** (Figure 22-Figure 23), with its strong midrib, water moves externally along the midrib and in the spaces between the scales, providing a film of water throughout the thallus (McConaha 1941).

Figure 35. ***Riccia sorocarpa*** thallus section showing ventral rhizoids, dorsal midribs, and internal photosynthetic layer. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 36. ***Targionia hypophylla***, a thallose liverwort with pegged and smooth rhizoids and scales. Photo by Des Callaghan, with permission.

Figure 37. ***Asterella saccata*** showing scales around the thallus margin. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Pallavicinia lyellii***, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Des Callaghan, with permission.

Figure 39. ***Monoclea*** cf. ***gottschei*** with the salamander ***Oedipina gracilis***. This liverwort is a simple thallus lacking the complex scales and two types of rhizoids, but clearly having a waxy surface. Photo by William Leonard, with permission.

Figure 40. ***Neohodgsonia mirabilis*** with archegonial heads in New Zealand, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Odontites, through Creative Commons.

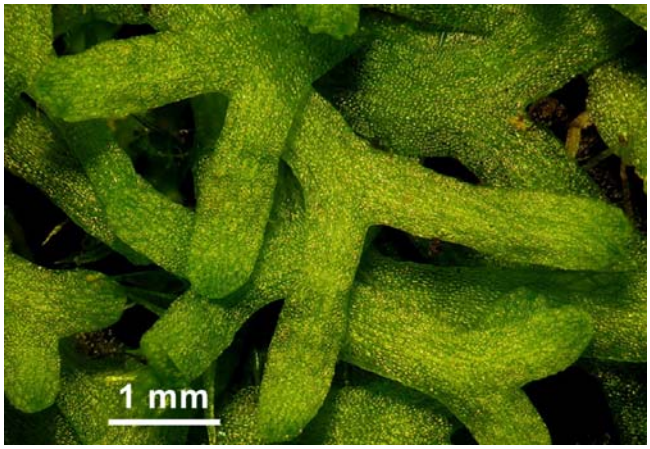

Figure 41. ***Riccia fluitans***, an aquatic species with no rhizoids or scales. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 42. Cross section of thallus of ***Riccia fluitans***, an aquatic species with no rhizoids or scales; note the large air spaces for gas exchange and flotation. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

In ***Preissia*** (Figure 30), it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that ***Riccia*** (Figure 43), a common inhabitant of ephemeral habitats such as flood plains, absorbs water by capillary action among the rhizoids and the lower surface of the thallus. The thallus rolls or folds when it is dry, thus exposing the rhizoids, scales, and/or cilia. These serve both to absorb water and to provide a reflective surface that protects the **chlorophyllous** (photosynthetic) cells of the thallus. In others, a crystalloid crust serves a similar function of reflectance.

Fungal Partners

Despite their roles in anchorage (smooth rhizoids) and conduction (pegged rhizoids), it seems that smooth rhizoids have a major role in the **endosymbiosis** (internal partnership) of fungi (Pressel *et al*. 2010, 2012; Duckett *et al*. 2013). Our understanding of the value of this partnership is meager. In other plants, fungi serve to increase absorptive surface area and often tap into the roots of a tracheophyte, transferring carbohydrates from plants that reach the canopy to plants that are in the low light beneath them. Such a role remains unknown in the bryophytes, but I am confident that we shall discover that at least some species have this advantage. After all, these partners have been around much longer than the flowering plants, known as **hemiparasites**, that have succeeded in developing this life style. In the leafy liverworts, infections occur exclusively through rhizoids with the Ascomycete ***Rhizoscyphus ericae*** as partner (Read *et al.* 2000; Pressel *et al*. 2008a, c). This is a widespread fungus that lacks host specificity. Fungal partnerships are discussed in more detail below under "Mosses and Leafy Liverworts."

Main Thallus Structure

Midribs: Seeing the midribs in valleys (Figure 35, Figure 43) makes me think that water is directed from the thallus surface to the midrib in some species. I have to wonder if water is absorbed more easily there. Once the water enters the midrib cells, it can be carried to more distant parts of the thallus more quickly than by travelling through other, shorter thallus cells.

The rib of ***Lunularia cruciata*** (Figure 44-Figure 45) has parenchymatous cells in which plasmodesmata-derived pores are grouped in small, sparse fields, particularly on transverse oblique walls (Giordano *et al*. 1989). This suggests that the rib cells may be able to transport water and other substances through the ends of cells. These longer cells should, then, move water faster than crossing the many walls of the hyaline parenchyma (Figure 46). Giordano and coworkers suggested that the reticulate cells may serve a water-holding role and facilitate lateral distribution by both **symplastic** (within protoplasm) and **apoplastic** (outside the protoplasm, in intercellular spaces) conduction of substances arriving by way of the rib. They suggest this mechanism may be present in all members of **Marchantiales** with this thallus construction.

Figure 43. ***Riccia nigrella*** showing valleys with midribs that could be used to direct water into the thallus. Photo by Des Callaghan, with permission.

Figure 44. ***Lunularia cruciata*** indicating rib area (**arrows**). Photo by Luis Nunes Alberto, through Creative Commons.

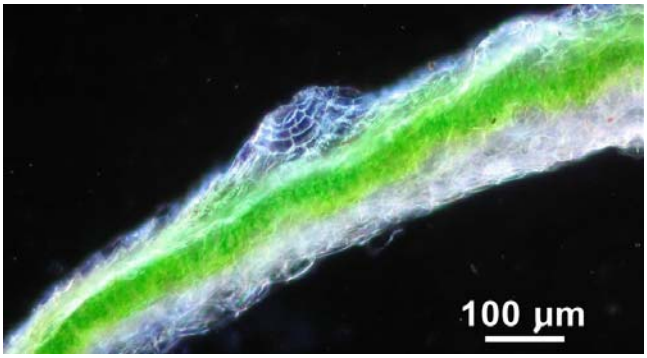

Figure 45. ***Lunularia cruciata*** thallus showing pore and hyaline parenchyma cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Rolling Thallus: Midribs may also facilitate rolling of the thallus by creating a crease through the middle of the plant (compare Figure 43 to Figure 47). Rolling conserves water, but at the same time it exposes the ventral surface where scales help to conserve water (Figure 47). Such rolling is common in species of ***Riccia*** (Figure 69-Figure 70), often supplemented with hairs that cover the thallus.

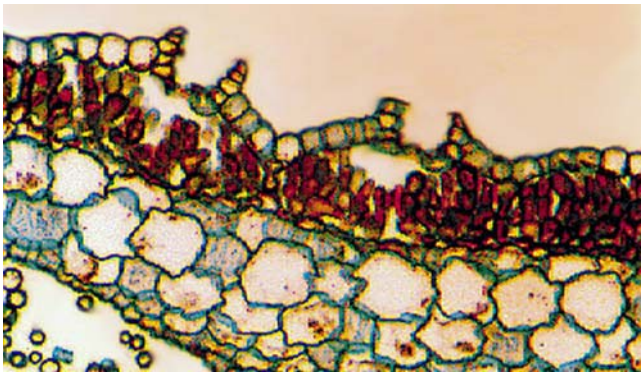

Figure 46. Cross section of ***Marchantia*** thallus, showing pore. Photo from Department of Botany Teaching Collection, Michigan State University, East Lansing, MI, USA.

Figure 47. ***Riccia nigrella*** with dry thallus folded at the midrib. Compare this to Figure 43. Photo by Michael Lüth, with permission.

Internal Conduction: The liverwort ***Lunularia cruciata*** (Figure 44-Figure 45) may exemplify a means for water movement between cells in thallose liverworts (Giordano *et al*. 1989). The thallus has **reticulate** (like network) **hyaline** (colorless) **parenchyma** (thin-walled) cells (Figure 45) with between wall thickenings, large **primary pit fields** (thin area in walls of many cells in which one or more pits usually develop) with numerous pores derived from **plasmodesmata** (narrow threads of cytoplasm that pass through cell walls of adjacent cells and allow communication between cells) on unthickened areas of walls.

Spongy Thallus

The spongy thallus of ***Riccia cavernosa*** looks like it should have an important adaptive value. The basal layer gives rise to a layer of irregular vertical column of chlorophyllose cells overtopped by colorless epidermal cells (*Riccia cavernosa* 2012). While these might seem to have functions similar to those of ***Exormotheca***, instead some of these epidermal and chlorophyllose cells collapse, creating large air spaces at several levels in the tissue of the thallus. The light that reflects from these cavities has a glistening appearance. But does this sequence of events provide any advantage to the plant? At first glance, it looks very much like a sponge, but at a much smaller scale.

The basal pad of isodiametric cells gives rise to a layer of irregular vertical columns of chloroplast containing cells, topped by colorless oval epidermal cells (*Riccia cavernosa* 2012). But early in development, large air spaces develop at several levels in this tissue due to the collapse of some of the epidermal and chlorenchyma cells. The light reflecting inside these cavities gives the thallus a characteristic glistening appearance.

Cuticle

For many years we considered the cuticle to be absent in bryophytes, with scattered references referring to them, but with no definitive data on their surface chemistry. However, not only are waxy cuticles present, but waxes are present on the leaves and thalli, albeit in less noticeable quantity than in tracheophytes. In fact, Brockington *et al*. (2013) considered the cuticle in the thallose liverwort ***Marchantia polymorpha*** (Figure 22) to be "an overlooked innovation in land plants."

Knowing that ***Marchantia polymorpha*** has a cuticle, one should not be surprised that the shiny thallose liverwort ***Monoclea gottschei*** (Figure 39) and the hornwort ***Notothylas orbicularis*** (Figure 48) have an **osmiophilic layer** (refers to lipid-containing bodies; a cuticle) with structural resemblance to that of early developmental stage tracheophyte cuticles (Cook & Graham 1998).

Figure 48. ***Notothylas orbicularis***, a species with a demonstrated osmiophilic layer, *i.e.* cuticle. Photo by Michael Lüth, with permission.

What emerged as more interesting in this study is that not all of these bryophyte versions are created equal. In the liverwort ***Monoclea gottschei*** (Figure 39) the layer is nodular, in the hornwort ***Notothylas orbicularis*** (Figure 48) it can be either nodular or sheetlike, and in ***Sphagnum fimbriatum*** (Figure 49) it is sheetlike with regular ridges that run parallel to the edges of the "thalli" (Cook & Graham 1998). It appears that cuticle is ancient, and Cook and Graham suggest that it may have arisen before the charophycean algae and bryophytes diverged from their common ancestor.

The thallose liverwort ***Plagiochasma rupestre*** (Figure 60) has a non-wettable thallus endowed with hydrophobic wax globules, preventing it from absorbing water through its surface (Kürschner 2004). Instead, it uses the pegged rhizoids for water uptake, a phenomenon that may be common to all members of **Marchiantiales**. This dorsal surface wax may have an important role in preventing water logging in the underlying air chambers.

Figure 49. ***Sphagnum fimbriatum***, a species with a cuticle. Photo by Michael Lüth, with permission.

The presence of a cuticle on the upper surface of a thallose liverwort raises the question of water absorption in these species. One might surmise that it occurs through the ventral surface, facilitated by the scales and rhizoids. Presumably there is no cuticle on that surface, but that does not yet seem to have been demonstrated.

In the **Polytrichaceae**, waxes may serve a different function. Rather than keeping water in, the leaves of these species must keep water out to permit maximum photosynthesis (Figure 50) (Clayton-Greene *et al*. 1985). Their lamellae provide extra photosynthetic tissue, but water can become trapped there due to the capillary spaces. This protection from water is further enhanced by the rolled margins (Figure 51) of species like ***Polytrichum juniperinum*** (Figure 52).

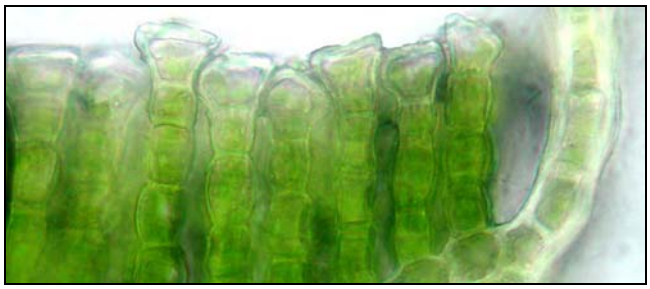

Figure 50. ***Polytrichastrum pallidisetum*** showing leaf lamellae where photosynthesis occurs. Note thickened end walls that help keep water from entering capillary spaces between lamellae. Photo by Michael Lüth.

Figure 51. ***Polytrichum hyperboreum*** showing inrolled leaf margins that cover the lamellae and protect them from water logging in the capillary spaces. Photo by Michael Lüth, with permission.

Figure 52. ***Polytrichum juniperinum*** showing lamellae and leaf edge that is rolled over them to help keep water out of the capillary spaces. Photo by John Hribljan, with permission.

Pores

The wonderful ventral efficiency of rhizoids and scales is often challenged by a dorsal surface that does little to conserve water. In fact, this dorsal surface water loss may facilitate the movement of water and nutrients through the plant, as it does in leafy tracheophytes. The pores on the dorsal surface function much as do the stomata of tracheophyte leaves in losing water (Figure 46, Figure 58). Maier-Maercker (1982) found that ***Conocephalum conicum*** (Figure 24) loses water through transpiration from these dorsal thallus pores (Figure 53), accumulating radioactively labelled ions in the cells surrounding the air pores.

The single-layered leaves of mosses and leafy liverworts preclude the presence of stomata there as they would provide only a hole through the leaf, hardly a useful character. Even multicellular layers of moss leaves have no use for stomata because there is no chamber where the gases may gather. But thallose liverworts meet those two requisites – multiple cell layers (Figure 54) and chambers internally (Figure 55). Furthermore, as mentioned above for ***Marchantia polymorpha*** (Figure 22), the thallus has a cuticle that can at least to some degree repel water. Hence we might presume that it likewise is somewhat resistant to gas exchange, creating a problem for photosynthesis.

Raven (2002) provided evidence that stomata evolved from pores of an epidermis over plant organs at least three cell layers thick, with intercellular gas chambers, and with a cuticle. In this anatomical arrangement, the presence of pores most likely confers an adaptive advantage for photosynthesis.

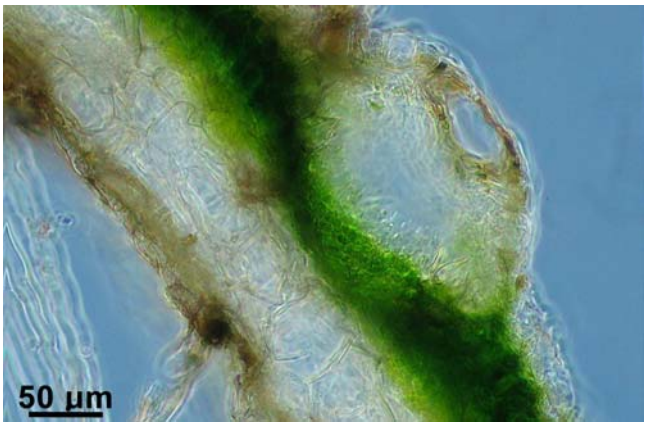

Figure 53. ***Conocephalum conicum*** pore section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 54. ***Conocephalum conicum*** photosynthetic cells under epidermis, showing thallus that is more than three cell layers thick. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

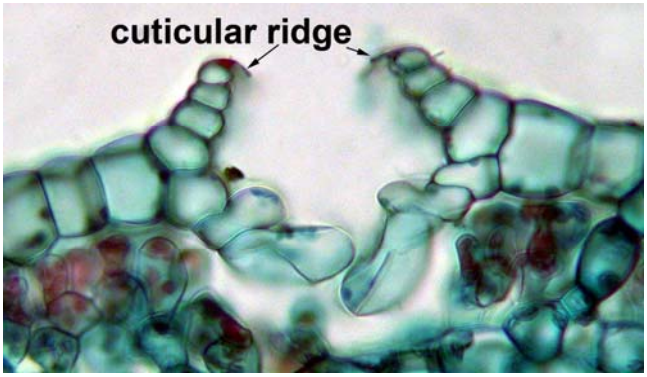

Figure 55. ***Marchantia polymorpha*** thallus pore in longitudinal section, showing cuticular ridge. Cells stained with purple are photosynthetic cells. Note the chamber beneath the pore. Photo by George Shepherd, through Creative Commons.

In some cases, thalloid liverworts seem to lose great quantities of water, 2-3 times that of leaves of the weeping birch tree *Betula pendula* (McConaha 1941). Under extreme conditions, they transpire equivalent to their total content of water in an hour. One reason for this rapid transpiration rate is the areolation of the thallus that creates a large surface area where water can be lost. The pores in these thalli (Figure 56), permitting contact between outside air and internal moisture, have only limited ability to close, thus being a major source of water loss. McConaha (1941) claims that the ventral specializations compensate for the losses from dorsal areolation and pores. Proctor (1980) found that these areolate thalli have internal resistances similar to those of mesophytic leaves of flowering plants (Proctor 1980). As in the flowering plants, the water loss is correlated with pore size and density.

Figure 56. ***Marchantia chenopoda*** pores showing rim of cuticle projecting into the pore opening. The polygons outline the internal chambers that create the areolation. Photo by George Shepherd, through Creative Commons.

But the photosynthetic cells project into these chambers beneath the pores (Figure 55), and flooded cells cannot exchange gases freely. It should be no surprise then that the openings themselves prevent the entrance of water into the chamber. Their small size (Figure 56) contributes to this. In the absence of a wetting agent, the cohesive forces of water make the aggregation of water molecules too large to enter the holes. This smallness of the hole is further enhanced by the presence of a **cuticular ridge** (Figure 56-Figure 59) that not only narrows the entrance, but that also repels the water.

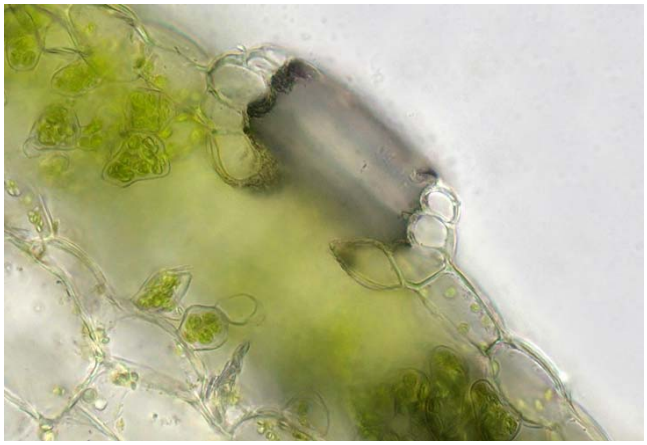

Figure 57. ***Marchantia polymorpha*** pore in longitudinal section. Photo by Walter Obermayer, with permission.

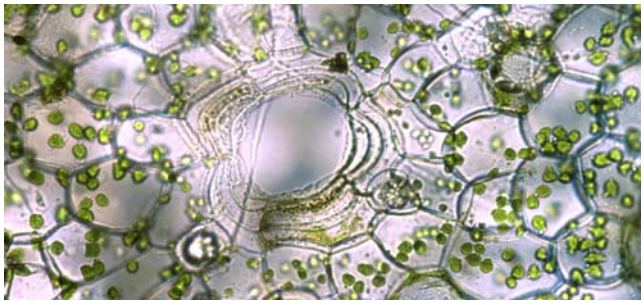

Figure 58. Pore opening in thallus of ***Cyathodium cavernarum***. Photo courtesy of Noris Salazar Allen.

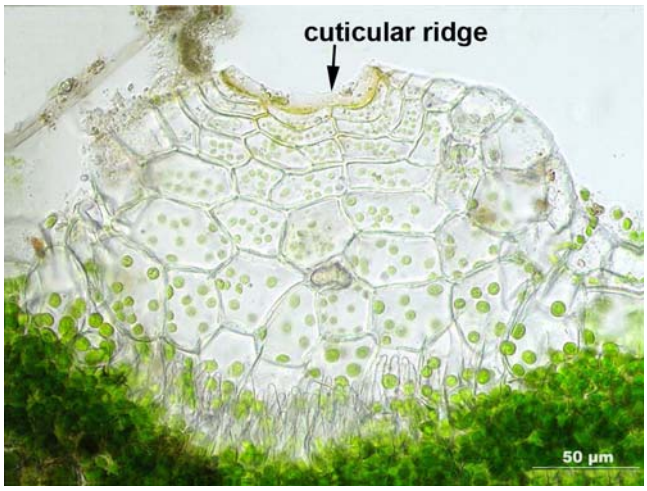

Figure 59. ***Conocephalum conicum*** pore longitudinal section showing the cuticular ridge. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Figure 60. ***Plagiochasma rupestre***, a thallose liverwort with no cuticular ridge on its pores, but with a waxy cuticle on the thallus. Photo by Michael Lüth, with permission.

Schönherr and Ziegler (1975) found that of the fourteen thallose liverwort species they studied, twelve of them have such **hydrophobic** (repelling water) ridges, and that **cutin** is present in these ridges. Furthermore, the researchers considered the pores in these species to be "perfect" in keeping water out of the thallus. ***Plagiochasma rupestre*** (Figure 60) and ***P. peruvianum***, on the other hand, lack such ridges and liquids are able to enter the thallus through the pores. While the waxes and small size of the holes keep water out, the water in vapor form within the thallus is able to escape through the pores, along with oxygen, while CO_2 enters. Therefore, the openings must maximize carbon gain per unit water loss (Raven (2002).

While these pores are an advantage for a hydrated, photosynthesizing thallus, they are a liability for a drying thallus due to the loss of water vapor. But at least some of the liverworts seem to be able to partially control the opening. This is accomplished by curving of the stack of cells surrounding the opening, creating partial closure. In ***Preissia*** (Figure 61-Figure 62, Figure 30), the barrel-shaped pores (Figure 62) change shape to accomplish control of water loss (Lepp 2008). When turgid with water, the cells at the bottom of the barrel keep the pore open, but when the conditions are dry, the cells lose their turgor and collapse, narrowing the opening at the bottom of this barrel. Those in ***Marchantia*** (Figure 55-Figure 57) behave similarly (Raven *et al*. 2005).

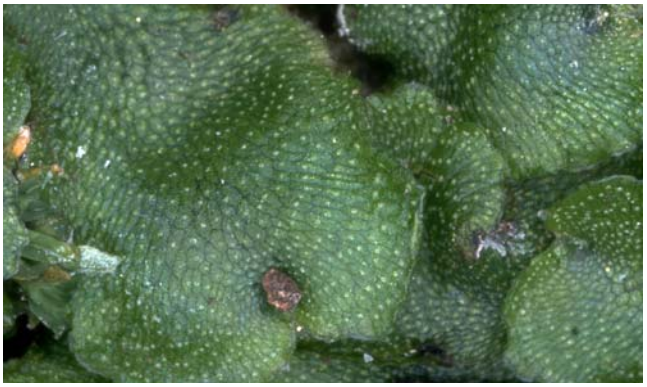

Figure 61. ***Preissia quadrata*** thallus wowing pores (light-colored dots). Photo by Jan-Peter Frahm, with permission.

Figure 62. ***Preissia quadrata*** thallus showing pores with cuticular ridges. Photo by Kristian Peters, with permission.

Archegoniophores and Antheridiophores

In thallose liverworts, the horizontal orientation cannot serve as a model for water movement in the vertical **archegoniophore**. As determined by Duckett *et al*. (2013), the archegoniophore has more efficient water movement than the stems of mosses. They attribute this to the efficiency of movement through the rhizoids and capillary

spaces among them, as well as the hydrophobic nature of the thallus surface surrounding these rhizoids (Figure 63).

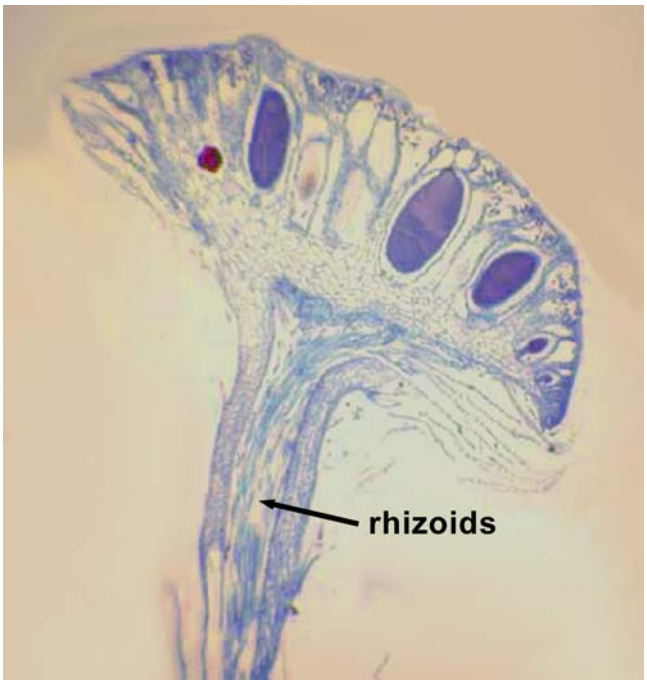

Figure 63. ***Marchantia polymorpha*** antheridial head showing location of rhizoids within the antheridiophore. Photo from Botany website of the University of British Columbia, BC, Canada, with permission.

The importance of this rhizoid-thallus combination for the archegoniophore is suggested by comparing its response to drought with that in mosses. For example, ***Marchantia*** (Figure 64) archegoniophores and heads can remain fully hydrated for several hours in full sunlight at 20-30°C while the shoots of neighboring ***Polytrichum commune*** (Figure 65) with their bases in standing water become wilted and must have added rainwater to recover (Duckett *et al.* 2013), suggesting an efficient system of transport in the archegoniophore.

Figure 64. ***Marchantia polymorpha*** archegoniophore and archegonial head. Note rhizoids along stalk (archegoniophore) where they emerge from the folded thallus that makes the stalk. Photo by George Shepherd, through Creative Commons.

Figure 65. ***Polytrichum commune***, a moss that wilts in full sun despite its wet substrate and colonial habit. Photo by Michael Lüth, with permission.

Duckett *et al*. (2013) suggest that the length of the archegoniophore is limited to a maximum of 7-10 cm (in ***Conocephalum***; Figure 66) because of the problems of air bubbles in the mucilaginous matrix surrounding the pegged rhizoids in the grooves of the archegoniophore, a condition analogous to an embolism in the vessels of tracheophytes (see Canny 2001 a, b).

Figure 66. ***Conocephalum conicum*** with tall archegoniophore. Photo by Adolf Ceska, with permission.

Antheridiophores provide yet a different mechanism (Duckett & Pressel 2009). Present only in the genus ***Marchantia***, they present an antheridial head (Figure 67) on a stalk that is much shorter than that of the mature archegoniophore, rarely exceeding 30 mm. Rather than being hydrophobic, the heads are highly hydrophilic and absorb raindrops much like a sponge. Whereas upward flow occurs in the stalk during dry periods, downward flow carries the motile sperm toward the archegonia on immature (shorter) archegoniophores (Figure 68) during rainfall.

Figure 67. ***Marchantia polymorpha*** with antheridial heads where water is absorbed like a sponge. Photo by Rudolf Macek, with permission.

Figure 68. ***Marchantia polymorpha*** young archegoniophores that receive sperm from temporarily taller antheridiophores. Photo by Rudolf Macek, with permission.

Dormancy

Volk (1984) found that when ***Riccia*** (Figure 69-Figure 70) has less than 150 mm of rainfall per year, it requires other means to survive, and it seems that dehydration/dormancy is the solution (Figure 69-Figure 70). Some thallose ***Riccia*** species are able to survive up to 7 years in this dehydrated state, enduring temperatures up to 80°C. The annual species compensate for this water loss by producing huge numbers of spores, taking advantage of their ornamentation for distribution by animals.

Figure 69. ***Riccia sorocarpa*** in a fresh, active state. <www.aphotofauna.com>, with permission.

Figure 70. ***Riccia sorocarpa*** in a dry, dormant state. Photo by Michael Lüth, with permission.

Mosses and Leafy Liverworts

We typically think first about structural adaptations for water retention, so we will start there. Sarafis (1971) considered that ***Polytrichum commune*** (Figure 65) had four ways of controlling water loss:

1. Community level – gregariousness
2. Plant level – leaf density & size, plant height
3. Organ level – leaf movement and inrolling
4. Molecular level – wax on leaf surface

These all relate to structure, but internal structure and cellular level physiology are additionally important.

Bayfield (1973) considered that water loss in endohydric ***Polytrichum commune*** to be controlled by its leaf arrangement changes. This was accompanied by changes in water potential deficit of the shoots, with conduction being primarily internal under high evaporative flux and external under moderate flux. The ectohydric ***Racomitrium lanuginosum***, by contrast, has little control over its water loss.

After examining 439 taxa of pleurocarpous mosses, Hedenäs (2001) reported that most differences in taxonomic character states between environments relate to two functions: 1) water conduction and retention; 2) dispersal. Those characters that seem important for water relations relate to **stem central strand**, **leaf orientation**, **leaf costa type**, **alar cells**, **paraphyllia**, and **pseudoparaphyllia**. But if acrocarpous mosses (upright mosses with terminal sporophytes) had been included, surely many more characters might be added, as it is mostly acrocarpous mosses that occupy the most xeric of habitats.

One feature of structural adaptations is that many are plastic (Buryová & Shaw 2005). For example, **conducting strands** disappear in the liverworts ***Moerckia flotoviana*** (Figure 71) and ***Haplomitrium hookeri*** (Figure 72-Figure 73) under high humidity or liquid culture (Hébant 1977). **Hair points** (colorless, hairlike extensions at leaf tip) of ***Schistidium apocarpum*** (Figure 75) likewise disappear in humid conditions (Figure 75).

Figure 71. ***Moerckia blyttii***, a thallose liverwort that loses its conducting cells in wet habitats. Photo by Michael Lüth, with permission.

Figure 72. ***Haplomitrium hookeri***, a liverwort that loses its central strand in wet habitats. Photo by Des Callaghan, with permission.

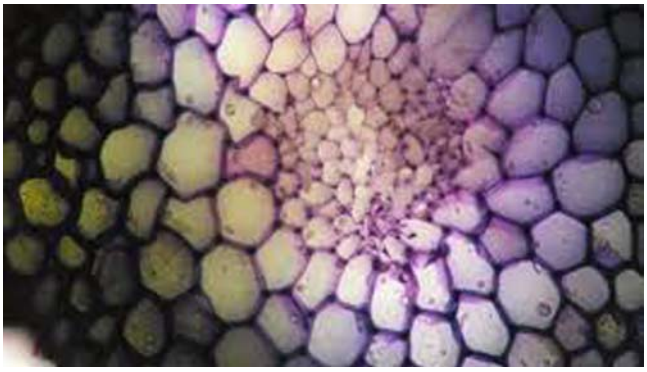

Figure 73. ***Haplomitrium*** sp. stem cross section with central strand that disappears in wet habitats. Photo by Rachel Murray and Barbara Crandall-Stotler, with permission.

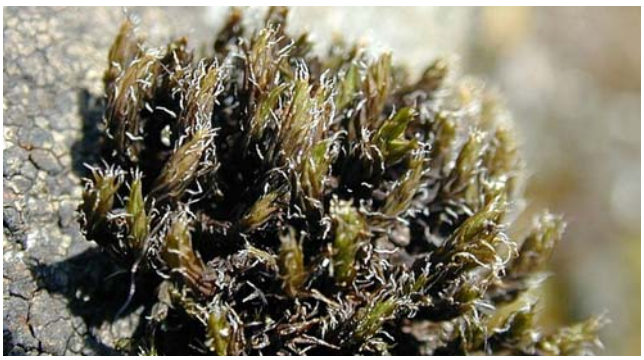

Figure 74. ***Schistidium apocarpum*** with hyaline hair points, on an exposed rock. Photo by Michel Lüth.

Figure 75. **Upper: Lower: *S. apocarpum*** without hyaline hair points in a more shaded or moist environment. Photo by Jan-Peter Frahm, with permission.

Rhizoids are less well developed or absent in wet conditions (Smith 1988), even in the same species. In ***Andreaea blyttii*** (Figure 76), increased moisture results in longer, wider leaves that are more curved with longer cells in the basal margin, wider **costae** (midrib of leaf), and longer stems, but with a decrease in number of leaves per stem (Heegaard 1997). Even in typically aquatic taxa such as ***Drepanocladus*** (*sensu lato*), leaves become longer, and falcation (leaf curvature) is lost in submersed leaves (Figure 77) compared to those grown out of water (Figure 78), and the reduced light results in greater **internode** distances (distance between leaf insertions) (Lodge 1959). A similar response is seen in ***Fontinalis*** (Figure 79). It is interesting that increases in salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.

Figure 76. ***Andreaea blyttii***, a moss that changes its leaf morphology in response to moisture changes. Photo by Michael Lüth, with permission.

Figure 77. ***Drepanocladus aduncus*** with straight leaves resulting from growing under water. Photo by Michael Lüth, with permission.

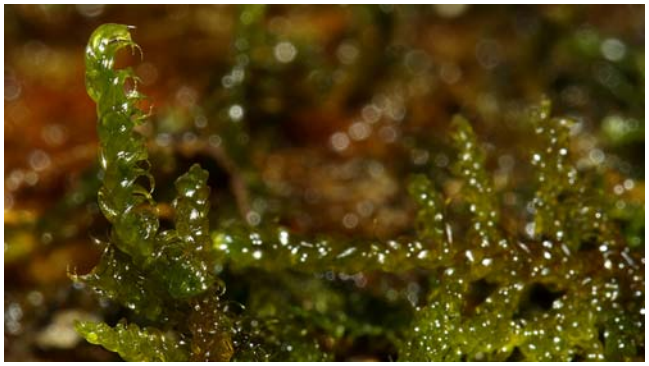

Figure 78. ***Drepanocladus aduncus*** with falcate leaves resulting from growing above water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 79. **Upper:** ***Fontinalis novae-angliae*** with normal submersed leaves. **Lower:** ***F. novae-angliae*** with leaves grown out of water, exhibiting an atypical falcate habit. Photos by Janice Glime.

Proctor (2010) reminds us that adaptations are subject to phylogenetic constraints and that entire clades may represent adaptations to desiccation. All plants must obtain water and CO_2, but their multiple ways that this can be achieved.

Growth Form

Growth form is important both for obtaining and retaining water. For example, ***Grimmia pulvinata*** (Figure 80) forms cushions. In this moss, and most likely others with this growth form, size matters. As the clump grows larger, the surface to volume ratio decreases as the larger cushion is accompanied by greater height in the center. This reduces exposed area for gas exchange, but it also reduces the portion exposed to the atmosphere for water loss. In ***Grimmia pulvinata*** the larger cushions have lower area-based evapotranspiration rates due to a higher boundary-layer resistance, but the relative water storage capacity per dry weight does not change (Zotz *et al*. 2000). Consequently, the hydrated period is considerably longer in larger cushions. And as predicted, the CO_2 exchange rate decreases with increasing size of the cushion, with both net photosynthesis and dark respiration decreasing.

Figure 80. ***Grimmia pulvinata*** showing cushion form that conserves water. Photo by Michael Lüth, with permission.

Living in **clumps** affects the ability to gain and to retain moisture. The cushion growth form decreases the surface to volume ratio, thus reducing surface water loss. Clump shape is important in this relationship, particularly in ameliorating wind effects (Proctor 1981; Zotz *et al.* 2000; Rice *et al*. 2001; Rice & Schneider 2004; Rice 2012). But for this system to work, the surface must be as smooth as possible. Greater roughness, resulting from protruding shoots, increases the turbulent air flow, thus increasing evaporation (Proctor 1981; Rice & Schneider 2004). A consequent advantage to the cushion growth form and its retention of water is the slowing the drying rate (Sand-Jensen & Hammer 2012).

Fortunately, this is a self-regulating condition. As a shoot emerges from the surface, the greater exposure and greater evaporation cause its growth to attenuate. Even herbivores might contribute to this evening, choosing the protruding branch because it is easier to munch on. Hence, the surrounding mosses are able to catch up in length, returning the clump to its smooth structure. Thus, moisture limitations create a more matted clump with a smoother surface, limiting turbulent flow and wind penetration into the clump (Longton 1979; Guerra *et al*. 1992; Nakatsubo 1994).

Nakatsubo (1994) examined the importance of the growth form of sub-alpine mosses in controlling their evaporative water loss. The xerophytic species were comprised of large cushions and compact mats. Mesophytic species from the coniferous forest floor were represented by smooth mats, wefts, and tall turfs. The evaporation rate per dry weight was much less in the xerophytic species than in the mesophytic species. However, when compared on a basal area, the evaporation rates were similar. One advantage of the xerophytic species was their ability to increase weight per basal area without increasing roughness.

The density of the clumps seem to be a plastic character that can be modified by the environment (Gimingham & Birse 1957; LaFarge-England 1996; Bates 1998; Rossi *et al*. 2001). For example, the endohydric ***Polytrichum juniperinum*** var. ***alpestre*** (Figure 81), when in humid habitats, forms a looser clump structure and greater roughness than when in drier habitats (Birse 1957).

Figure 81. ***Polytrichum juniperinum*** var. ***alpestre*** showing contacting leaves of adjoining shoots. Photo by Des Callaghan, with permission.

Elumeeva *et al*. (2011) set out to determine the important characters that maintained moisture in sub-Arctic bryophytes. They found that individual shoot properties seemed to have little effect on colony water retention capacity. That is, leaf cell wall properties, water retention capacity, and desiccation rate of shoots made little difference in the water relations of the colony. Rather, the colony desiccation rate was determined by the density of the water-saturated colony. The desiccation rate of the individual shoot had a marginally significant negative effect on the colony rate.

In ***Polytrichastrum formosum***, the plants are relatively tall and arranged in loose clumps. Nevertheless, the leaves of adjoining shoots touch, permitting water drops to be trapped by the resulting web. Drop size is an important consideration in conducting experiments using artificial rain. Raindrops usually range 0.5 mm (light rain) to 5 mm (heavy rain) (Best 1950; Brandt 1989; Yakubu *et al*. 2016). Using this size range, Zajączkowska *et al*. (2016) determined that clumps of ***P. formosum*** were able to retain almost 60% of the applied water. When water was applied to the tips, water ran down the shoots and continued to run down until about 2 minutes after the water application ceased. When a drop lands on a leaf, it is more likely to be trapped by the leaf axil or by a leaf. Thus these clumps are benefitted by the catchment web formed by the overlapping leaves.

With these clump advantages, we might ask why so many mosses use other growth forms that are less compact. But moisture is not the only need for the mosses. A compact nature reduces light penetration, reduces CO_2 diffusion into the clump, and increases shoot-to-shoot competition for nutrients (Bates 1989; Rice 2012).

Mulder *et al*. (2001) explored the role of species richness on biomass, then compared it when these communities were exposed to experimental drought. They found that under drought conditions biomass increased with greater species richness. They determined that the interaction was facilitative rather than niche complementarity or sampling effects. Survivorship increased for almost all species as richness increased, with the least drought-resistant species receiving the most benefit in biomass. Rixen and Mulder (2005) found similar results in the Arctic tundra.

Stems and Branches

Most stem and branch arrangements relate to growth form or life form (see Chapter 4-5 of this volume). However, in some cases there is internal or structural modification, exemplifying the plasticity of some bryophytes. For example, ***Philonotis fontana*** (Figure 82-Figure 83) exhibits variation among populations in leaf dimensions, whereas their cell dimensions show little response to differences in water regime or light level (Buryová & Shaw 2005).

Figure 82. ***Philonotis fontana***, a species whose leaf dimensions vary with habitat. Photo by Des Callaghan, with permission.

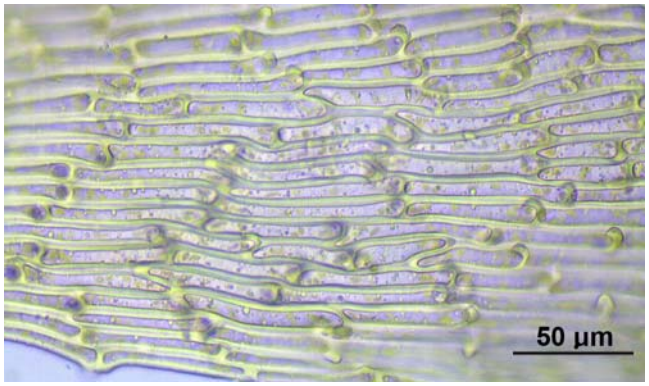

Figure 83. ***Philonotis fontana*** leaf lamina showing cells. These cells vary little in dimensions in different water or light regimes. Photo by Kristian Peters, through Creative Commons.

Overlapping leaves from neighboring shoots helps in the support of the mosses in a clump. In stems, the alternating layers of stiff and soft structures, such as those of the **Polytrichaceae**, the strength benefits from the **periodic component materials** (Vincent 2012) that occur

in many biological structures and provide stronger mechanical features (Dunlop *et al.* 2011; Fratzl *et al.* 2016). This layering provides the stem with both supportive strength and flexibility that prevents breakage. In ***Polytrichastrum*** and other members of the **Polytrichaceae**, the thicker cell walls surrounding the stem provide a higher bending strength (Niklas 1992), much like a paper straw compared with a paper lollipop stick. We also know that a lollipop stick made with twisted paper threads is stronger than a solid, non-twisted one, and that many trees likewise gain strength this way. This possibility needs to be explored in bryophytes.

Schröder (1886) considered the ability of moss stems to resprout from a dormant stem to be one method for withstanding prolonged drought. I had a similar experience with the aquatic moss ***Fontinalis dalecarlica*** (Figure 84). In this case, the moss was boiled for 14 hours a day for two weeks in the lab, then returned to the stream. One year later, new growth was present on this moss that was still attached to the numbered rock used in the boiling treatment. Such ability of stem tips to recover from environmental stresses have been largely overlooked.

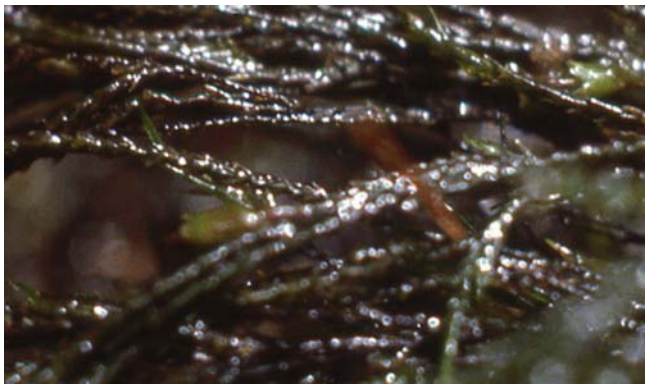

Figure 84. ***Fontinalis dalecarlica*** with from Fox Run, NH, where a plant similar to this produced a green leaf one year after being boiled for 14 hours a day for two weeks. Photo by Janice Glime.

Sphagnum*:** Li and coworkers (1992) examined the responses of two closely related ***Sphagnum hummock species, ***S. magellanicum*** (Figure 85) and ***S. papillosum*** (Figure 86), to distance from water surface and related these responses to structural and physiological adaptations of the two species. They found that both species increase growth in length as water becomes more available, *i.e.* as the distance from water level decreases. Likewise, dry mass is maximal under wet conditions, with new branches being a major mass contributor, especially in ***S. papillosum***. Furthermore, while experimenting with effects of distance from water on ***S. magellanicum*** and ***S. papillosum***, Li and coworkers found that dry conditions result in wider stems (Figure 87), with thicker hyaline layers (Figure 88-Figure 89), than stems with apical capitula near the water surface (Figure 90), presumably increasing both absorption and water-holding ability.

Sphagnum has pores in its stem (Figure 90), in most species, and has very rapid movement of water externally up the stem by capillary action, adapting it for its annual cycle of being stranded well above water level. Some species of ***Sphagnum*** have special **retort cells** (Figure 91) on the stems for absorbing water (Figure 91).

Figure 85. ***Sphagnum magellanicum***, a hummock species with efficient water movement. Photo by Michael Lüth, with permission.

Figure 86. ***Sphagnum papillosum***, a species with inefficient water movement. Photo by David Holyoak, with permission.

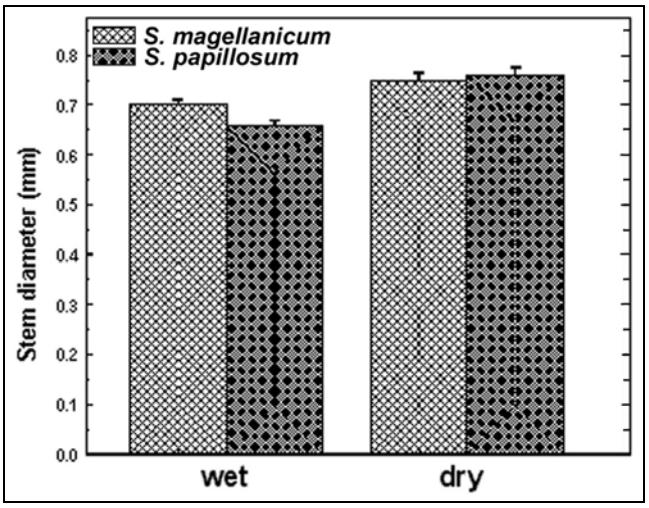

Figure 87. Effect of water level (water availability) on stem diameter in ***Sphagnum magellanicum***, a more desiccation-resistant species, and ***S. papillosum***, a more desiccation-tolerant species. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard errors; stem diameter in dry treatment is significantly greater (Figure 88) in both species. From Li *et al.* 1992.

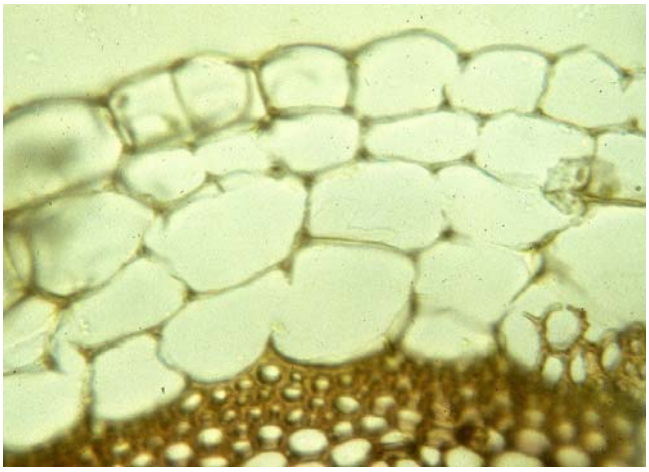

Figure 88. ***Sphagnum magellanicum*** stem at highest level (5) above water surface. Photo courtesy of Yenhung Li.

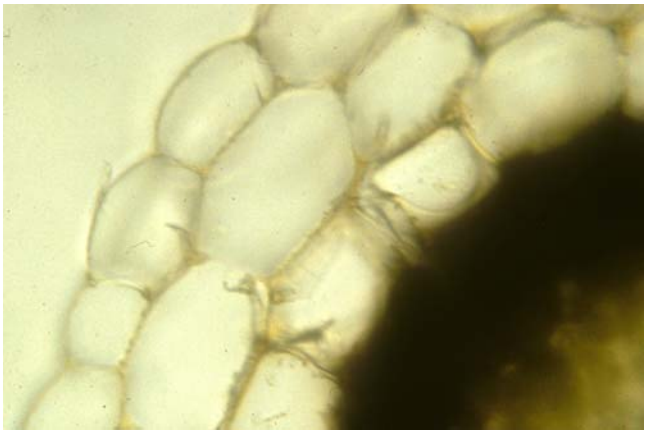

Figure 89. ***Sphagnum magellanicum*** stem at level 3 above water surface. Photo courtesy of Yenhung Li.

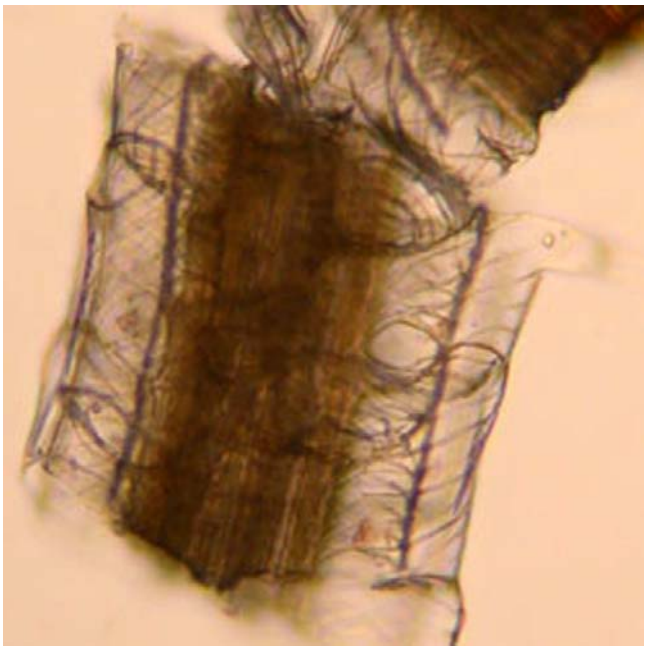

Figure 90. ***Sphagnum papillosum*** stem showing pores. The spiral thickenings of stem cells are unique in this moss. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

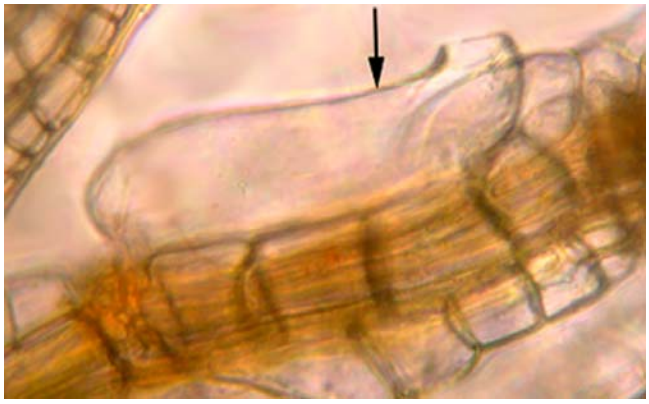

Figure 91. Retort cell (**arrow**) of ***Sphagnum***, showing pore. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Daniels (1989) found that while there is little differentiation between **spreading** and **pendant** branches (Figure 92-Figure 93) among ***Sphagnum*** plants growing in pools, hummock plants have more closely spaced **fascicles** (groups of branches), comparatively short spreading branches, and thin, closely appressed pendant branches (Figure 93). Pendant branches help to preserve stem water and maintain the wick effect as water level drops. Daniels determined that leaves of pendant branches on submerged plants photosynthesize actively, while those of hummock plants do not. He found that the two species growing in wet hollows (***Sphagnum cuspidatum***) or as wet carpets (***Sphagnum recurvum***) had the highest percentage of unbranched stems. The low hummock species ***Sphagnum papillosum***, on the other hand, had up to six **capitula** (terminal clump of branches) per stem; the two species growing in the high-humidity, shaded wet woodland exhibited intermediate degrees of branching.

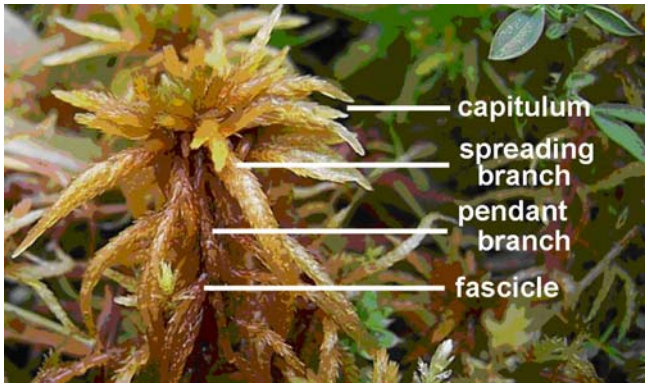

Figure 92. ***Sphagnum teres*** indicating two major branch types, compact capitulum, and joining of branches into fascicles. Photo by Michael Lüth, with permission.

Sphagnum magellanicum has greater ability to move and hold water than does ***S. papillosum*** (Li *et al*. 1992). Therefore, when they grow together in the same hummock, ***S. magellanicum*** will not only stay wet longer, but if it is dominant it will keep ***S. papillosum*** wet (Figure 94). However, it will fail to do so if ***S. papillosum*** is dominant (Figure 94). This is further supported by lab experiments in which ***S. magellanicum*** moved water farther externally in 20 hours than did ***S. papillosum*** (Figure 95; Figure 96).

Figure 93. Spreading branches and pendant branches on two hummock ***Sphagnum*** species. **Left: *S. magellanicum***. **Right: *S. papillosum***. Photos courtesy of Yenhung Li.

Figure 94. Predominately ***Sphagnum papillosum*** (**olive colored**) lower on the hummock (**left side of picture**) causes both species to be dry, whereas predominately ***S. magellanicum*** (**red**) higher on the hummock (**right side of picture**) causes both species to be wet. Photo by Janice Glime.

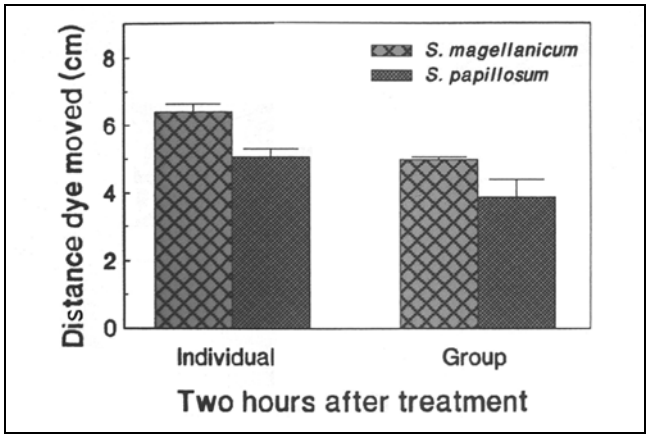

Figure 95. Comparison of distance travelled by dye in two ***Sphagnum*** species from lower (***S. papillosum***) and higher (***S. magellanicum***) in the hummock after 20 hours. Group refers to those kept together at field density with half of each species. From Li *et al*. 1992.

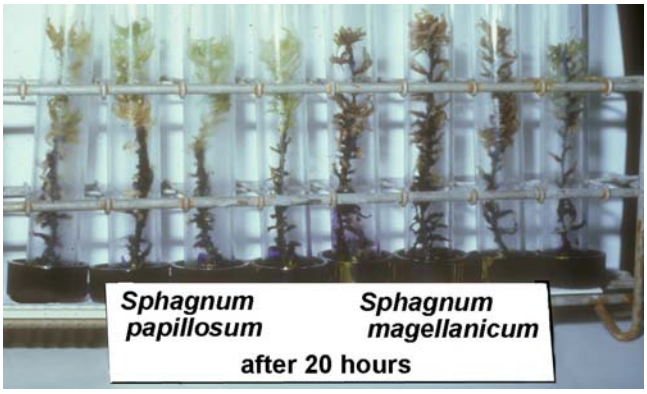

Figure 96. Comparison of upward transport in a low (**left**) and high (**right**) hummock species of ***Sphagnum***. Movement of water is indicated by purple dye. Photo courtesy of Yenhung Li.

Central Strand

In addition to the structural adaptations of stems and branches already described, the vascular system itself may be modified. The **central strand** (Figure 97) is typically composed of hydroids that are elongated and impose fewer cell end walls through which water must travel. Hébant (1973) found that variation occurred in the vascular elements, particularly in length and diameter, degree of inclination of end walls, and structure of the walls themselves. For example, whereas walls of hydroids are usually thin, they can be very thick, as in the swollen walls of hydroids in the setae of ***Dicranum scoparium*** (Figure 98) or the lateral walls of hydroids in the gametophyte central strand of the **Polytrichales** (Figure 99). But insufficient data exist to relate these variations to adaptive function.

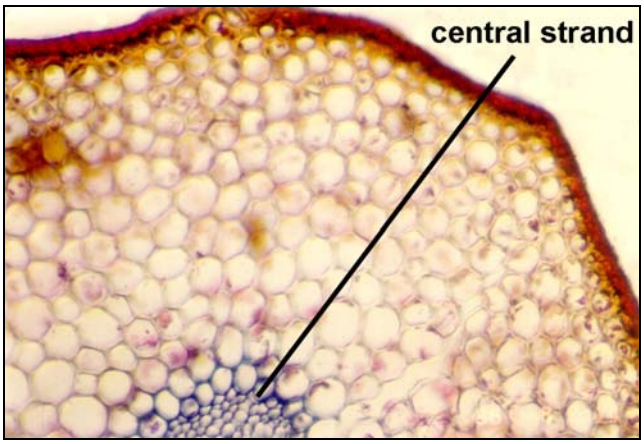

Figure 97. Stem cross section of ***Rhizogonium*** showing narrow cells of central strand. Photo courtesy of Isawo Kawai.

Using several references for comparison, Hébant (1977) showed that the number of hydroids within the ***Polytrichum commune*** central strand (Figure 99) can vary with habitat, following an apparent moisture gradient. In a pseudo-alpine grassland he reports 900 hydroids in the central strand, peat bog 400, cultivated in artificial peat 280, and cultivated under water 70. There is no clear indication as to how these numbers affect the rate of conduction, but one would presume that more hydroids conduct more water.

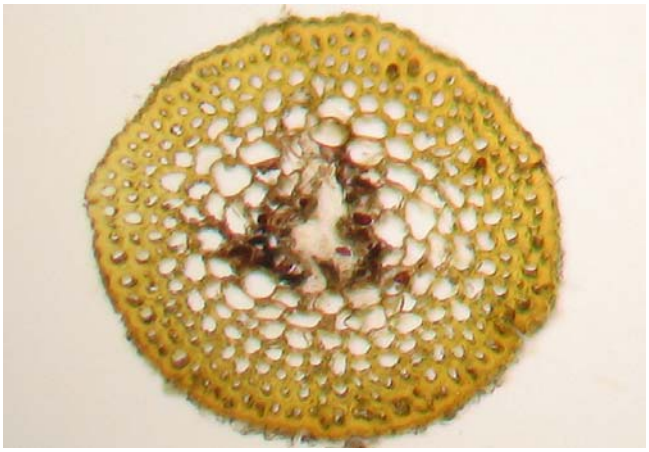

Figure 98. ***Dicranum scoparium*** seta cross section showing hydroids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Although in general, leafy liverworts lack conducting tissues in both leaves and stems (Crandall-Stotler 2014), ***Haplomitrium*** seems to be an exception. At least it possesses a differentiated central strand (Figure 100). But there seem to be no experiments to demonstrate that this actually serves as conducting tissue.

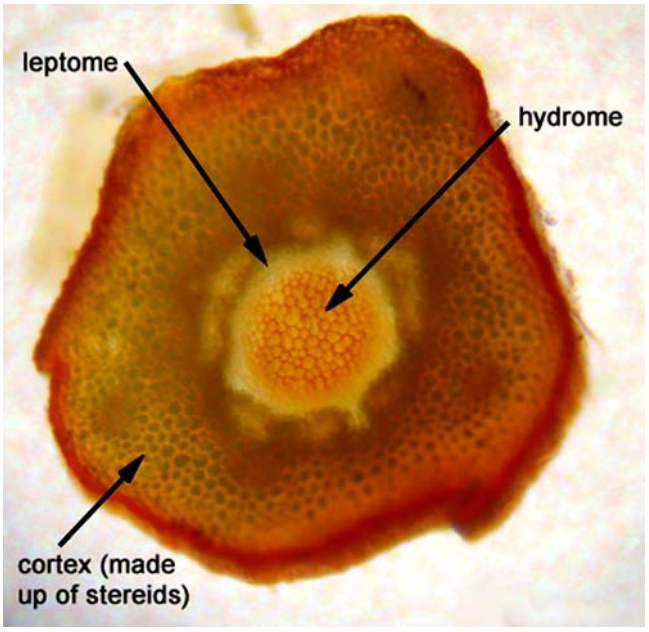

Figure 99. ***Polytrichum commune*** stem cross section showing central strand. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Waxes

Bryophytes leaves have frequently been described as lacking a cuticle. However, this ancient concept has proven to be false. Even leafy liverworts can have a cuticle. The details of the leaf cuticle will be discussed in the next subchapter, but we need to consider how such a cuticle might affect the whole plant water movement. Loss of water from leaves can create a transpiration stream that draws water upward, but in most bryophytes the greater movement of water is external. Hence, it is not surprising that little is known of the effects of a transpiration stream on water movement in bryophytes. It would be interesting to know if stems have a cuticle, but I am aware of no studies that isolated the stems to look for it. For now, we will concentrate on other aspects of water movement.

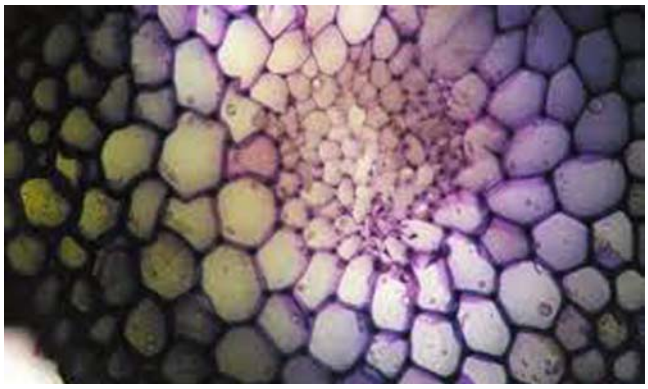

Figure 100. ***Haplomitrium*** stem cs showing thin-walled central strand. Photo by Rachel Murray & Barbara Crandall-Stotler, with permission.

Rhizoids and Tomentum

Rhizoids and **tomentum** (layer of matted woolly down on surface of plant; Figure 101) are adapted for water uptake. Pressel and Duckett (2011) found that rhizoids of all representatives they tested in **Polytrichales**, **Dicranales**, and **Bryales** (Figure 102) were **hydrophilic** (tendency to be wetted by water). For example, there is a sharp contrast between the leaves with a waxy cuticle in **Bartramiaceae** (Figure 103) and the highly hydrophilic tomentum-forming rhizoids (Figure 103) with papillae.

Mosses with dense rhizoids or **tomentum** (Figure 101-Figure 103) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that ***Bryum pseudotriquetrum*** (=*Bryum algens*; Figure 102), with a dense rhizoidal tomentum (Figure 102), held significantly more water than colonies with sparse rhizoids. But the tomentose form lost water more rapidly per unit dry mass than did the ones with sparse rhizoids. Could this be attributed mostly to loss of water from the tomentum? In ***Schistidium antarctici*** (Figure 104), the xeric form has less densely packed shoots and thicker cell walls that maintain lower water content than the high-water-holding-capacity hydric turf form. Mosses in Smith's study took several times longer to drop to minimal water contents than did lichens in the same conditions.

Figure 101. ***Rhizomnium magnifolium*** showing dense brown rhizoidal tomentum on lower half of stem. Photo by Michael Lüth, with permission.

Figure 102. ***Bryum pseudotriquetrum*** (**Bryales**) showing dense rhizoidal tomentum along stem. Photo by Misha Ignatov, with permission.

Figure 103. ***Breutelia chrysocoma*** (**Bartramiaceae**) showing rhizoidal tomentum. Photo by Michael Lüth, with permission.

Figure 104. ***Schistidium antarctici***, a moss that becomes morphologically modified by moisture conditions. Photo courtesy of Rod Seppelt.

In acrocarpous mosses, rhizoids are produced all the way around the base of the stem, serving on the lower parts for anchorage, and in mosses like the **Polytrichaceae**, for limited conduction (Odu 1978). Rhizoids further up the stem provide capillary spaces that can both store water and facilitate movement. In pleurocarpous mosses, rhizoids appear only on the side of the stem (Figure 105) toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In ***Fontinalis*** (Figure 106), where rhizoids have a critical function in anchorage, and this aquatic moss may encounter its substrate in any direction from the stem, the individual rhizoids grow in a spiral (Figure 107) until they encounter the substrate, then form multiple branches (Figure 108) in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).

Figure 105. ***Hygroamblystegium fluviatile*** rhizoids on one side of stem. Photo by Janice Glime.

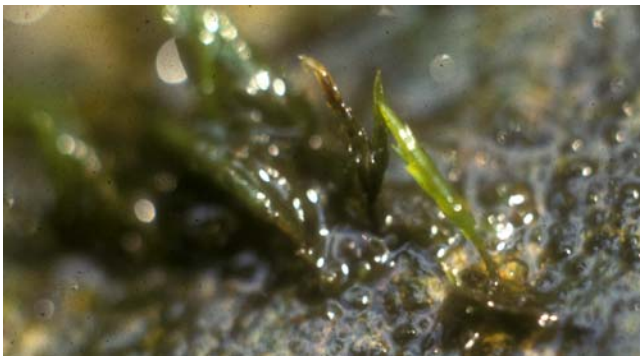

Figure 106. ***Fontinalis novae-angliae*** cemented to the rock by its rhizoids. Photo by Janice Glime.

Figure 107. ***Fontinalis squamosa*** rhizoids growing in a spiral where they are suspended above the substrate. Photo by Janice Glime.

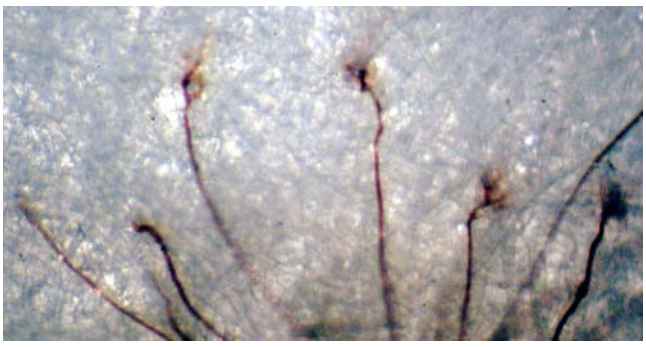

Figure 108. ***Fontinalis squamosa*** rhizoid tips branching. Photo by Janice Glime.

Higuchi and Imura (1987) cultured three moss species to determine the effects of submersion on the rhizoid characters. The thickness, surface decorations, and positions where the rhizoids arise appear to be stable in altered moisture conditions, but in ***Macromitrium gymnostomum*** the mucilage that is present in terrestrial cultures is lost in water culture. Rhizoids generally are not produced on submersed mosses in standing water (Odu 1978), perhaps because ethylene, which inhibits their development, cannot escape easily. This conserves energy, because it would seem that they are needed neither for anchorage nor absorption and conduction.

Surprisingly, Trachtenberg and Zamski (1979) found a cuticle on the rhizoids of ***Polytrichum juniperinum***, (Figure 109) sharply contrasting with roots and root hairs of tracheophytes, which serve as absorbing organs and have no waxy cuticle. This suggests that they may play little role in water uptake, but rather prevent water loss to the substratum. This raises questions about how widespread this cuticle is on rhizoids of other taxa and how it affects the capillary action they might otherwise afford. Perhaps they play only a role in conservation of water and not in its uptake. Or are these cuticles designed to provide capillary spaces that hold water around the rhizoids and facilitate uptake?

Figure 109. ***Polytrichum juniperinum*** males, a moss that has a cuticle on its rhizoids. Photo by Jan-Peter Frahm, with permission.

It is noteworthy that both leafy liverworts ***Haplomitrium*** (Figure 72-Figure 73) and ***Treubia*** (Figure 110) lack rhizoids (Figure 111) (Duckett *et al*. 2013). These unusual liverworts have leaves in three equal ranks and use underground stems (**rhizomes**) for anchorage and for fungal associations. All other liverworts produce **unicellular** (having only one cell) rhizoids (Figure 112). But only the thallose liverworts produce two types. Mosses, on the other hand, have multicellular rhizoids that branch (Figure 113).

Figure 110. ***Treubia lacunosa*** dorsal view. Photo by Jan-Peter Frahm, with permission.

Figure 111. ***Treubia lacunosa*** with sporophyte, showing absence of rhizoids. Photo courtesy of Jeff Duckett & Silvia Pressel.

Figure 112. ***Cephalozia*** sp. rhizoids showing that they are one-celled. Photo by Jan Fott, with permission.

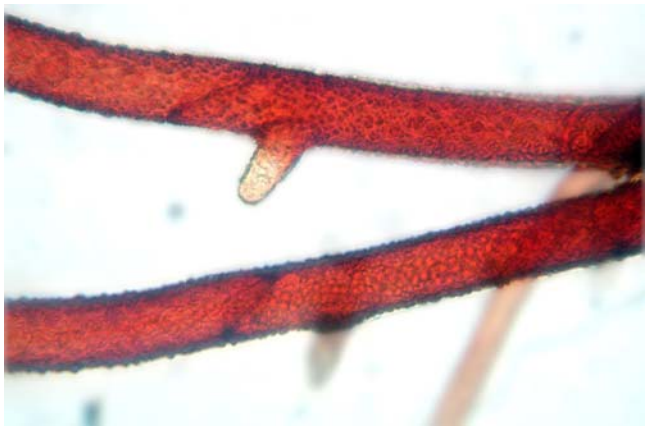

Figure 113. ***Bryum stirtonii*** rhizoid showing multiple cells, papillae, and branching. Photo by Michael Lüth, with permission.

Mucilage

Stem apices are protected by mucilage secreted by specialized hairs (Berthier *et al*. 1974). This mucilage seems to play a strong role in protecting the actively dividing tissue, permitting fragments to survive long periods of desiccation until they are able to grow again, and most likely playing a role in water retention, especially for the critical apical cells.

In liverworts and the moss ***Takakia*** (Figure 115) there are **slime papillae** (Figure 114) that may serve a water absorption/retention function as well. The leafy liverwort ***Haplomitrium*** (Figure 116) produces extensive mucilage on its rhizomes (Figure 116-Figure 117). It is interesting that these slime papillae appear in the green alga ***Coleochaete*** (Figure 118), the genus that seems most closely related to embryophytes, causing one to wonder if they may have been a prerequisite for land adaptation in early plants.

Figure 115. ***Takakia lepidozioides***. From the Herbarium of Hiroshima University, Hiroshima, Japan, with permission.

Figure 114. Stem of ***Takakia lepidozioides*** showing slime papillae. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 116. ***Haplomitrium gibbsiae*** leafy plant with mucous on its rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 117. ***Haplomitrium gibbsiae*** rhizome with mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 118. ***Coleochaete*** thallus, an extant green alga that has the most characters in common with bryophytes. Photo by Yuuji Tsukii, with permission.

The thallose liverwort ***Conocephalum conicum*** (Figure 19, Figure 24, Figure 53) has mucilage ducts in its thallus. Clee (1943) suggests that these may aid in water retention.

Capillary Spaces

Although several adaptations to holding water seem to exist [porose leaf cells, ridges, folds, sheathing leaf bases (Figure 119), rhizoids, tomentum], Proctor (1979) contends that most of the water is held in the larger capillary spaces between the moss shoots. Small amounts of dew that accumulate at the moss tip (Figure 120), *i.e.* the growing region, may be critical to survival (Lange 1969; Kappen *et al.* 1979). Hair points that wrap around the succeeding leaves above (Figure 121) help to deflect light and reduce evaporative loss by creating a diversion for air currents. Proctor (1980) experimented by removing hair points and found that when present they reduced water loss by 35% in ***Grimmia pulvinata*** (Figure 80) and ***Syntrichia montana*** (=*S. intermedia*; Figure 122). Thus far, it has been difficult to demonstrate that papillae afford any such advantage (Frey & Kürschner 1991). Nevertheless, in leaves they can act as a rapid capillary water movement system (Proctor 1979; Longton 1988; Pressel & Duckett 2011).

Figure 119. ***Bartramia ithyphylla*** illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth, with permission.

Figure 120. ***Campylopus introflexus*** showing water droplets at tips of plants. Photo by Jan-Peter Frahm, with permission.

Figure 121. ***Polytrichum piliferum*** illustrating leaf hairs that overlap the next leaf and help shield it from light, at the same time creating capillary spaces. Photo by Michael Lüth, with permission.

Figure 122. ***Syntrichia montana*** showing long hair points that can reduce evapotranspiration by up to 35%. Photo by Michael Lüth, with permission.

The leafy liverwort ***Trichocolea*** (Figure 123-Figure 124) is highly adapted to take advantage of capillary spaces. Its leaves are highly dissected and **paraphyllia** (leaflike appendages between the leaves; Figure 125) are abundant, permitting this species to act like a sponge. Zehr (1979) observed that it experienced only short-term vapor deficits in its moist habitat and thus was able to grow anytime temperatures were above freezing. Paraphyllia such as those in ***Hylocomium splendens*** (Figure 126-Figure 127) and ***Thuidium tamariscinum*** (Figure 128) create capillary spaces much like a tomentum. Other mosses such as **Mniaceae** utilize **paraphyses** (Figure 129) among the archegonia and antheridia to conserve water, using the same capillary principle.

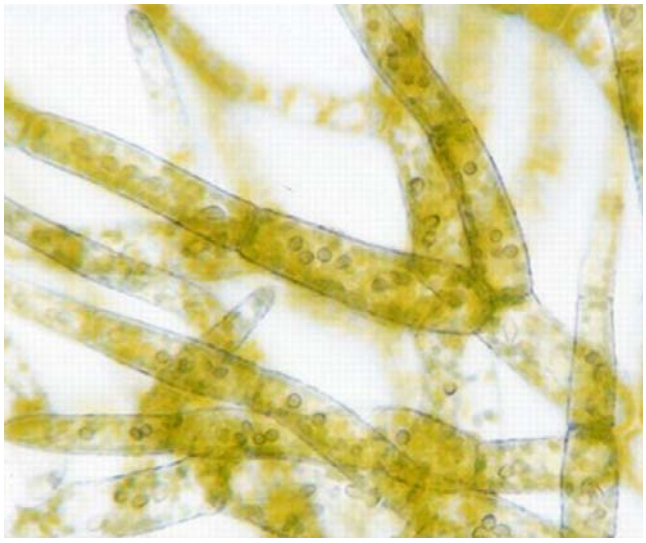

Figure 123. ***Trichocolea tomentella*** leaf cells. Photo by Malcolm Storey from Discover Life <www.discoverlife.org>, through Creative Commons.

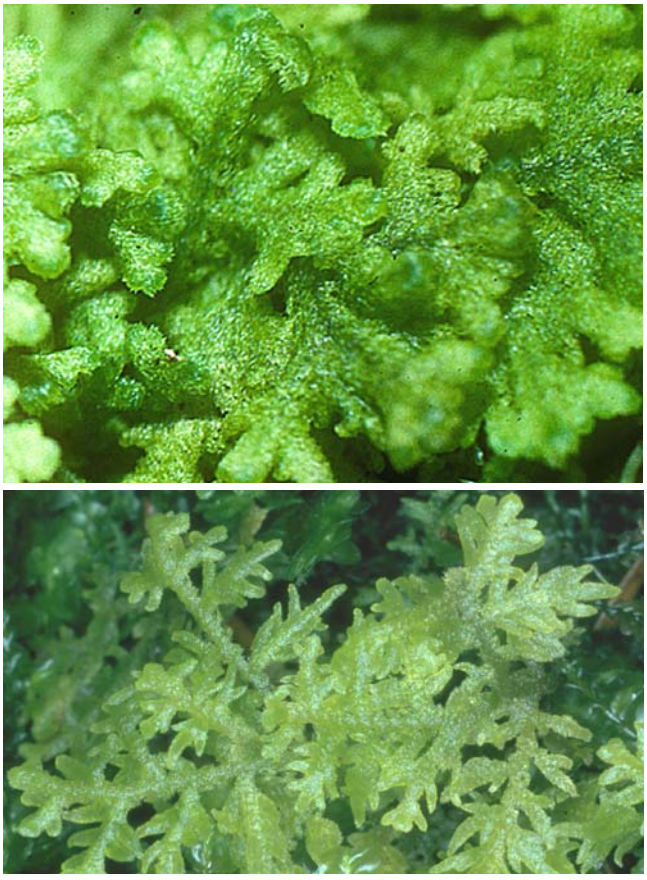

Figure 124. ***Trichocolea tomentella***, a leafy liverwort with finely divided leaves and paraphyllia. **Top:** dry. Photo by Janice Glime. **Bottom:** wet. Photo by Jan-Peter Frahm, with permission. Note the numerous capillary spaces afforded by the filamentous divided leaves.

Figure 125. ***Thuidium recognitum*** showing branched paraphyllia on the stem and branches. Photos by Michael Lüth (**upper**) and Paul Davison (**lower**), with permission.

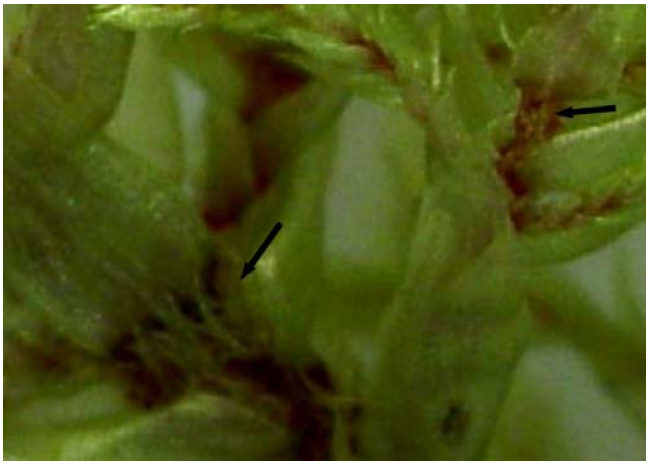

Figure 126. ***Hylocomium splendens*** showing paraphyllia on stem. Photo by Rosalina Gabriel, with permission.

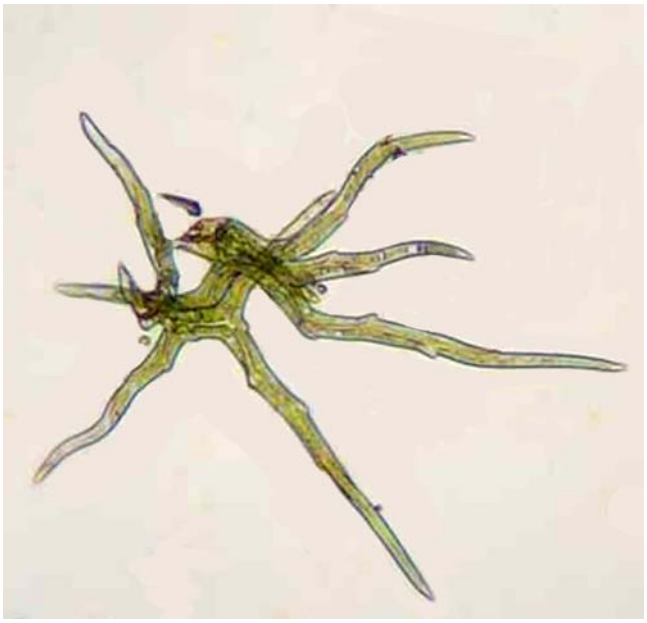

Figure 127. ***Hylocomium splendens*** paraphyllia. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Figure 128. ***Thuidium tamariscinum***, showing paraphyllia on stem (**arrows**). Photo by Brian Eversham, with permission.

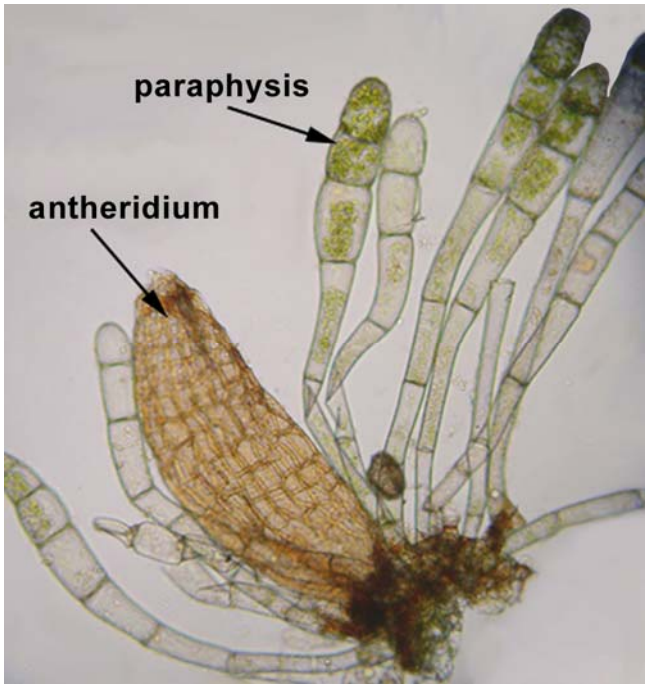

Figure 129. ***Plagiomnium insigne*** antheridia and paraphyses that create capillary spaces. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Fungal Partners

Fungal partners associated with roots have been termed **mycorrhizae**, and the same term is applied to fungi that serve as fungal partners to bryophytes. The existence of these relationships has been overlooked until recently, although we have recognized for quite some time that many bryophytes had fungi associated with them. Hence, our knowledge of their importance to the bryophyte is meager. It is likely that they serve a similar role to that in tree roots in scavenging a wide area for water, minerals, and perhaps organic nutrients. But I would also consider it likely that at least some of them play a role similar to that in the **hemiparasites** such as Indian pipe (*Monotropa uniflora*). That is, for those bryophytes living in dense shade, they could find a third partner that has more access to light – a leafy tracheophyte – that provides photosynthate that can be transferred from the tracheophyte, by way of the fungus, to the bryophyte. I am afraid I can see no substance that is likely to be produced by the bryophyte that is useful to the tracheophyte, making the bryophyte also a hemiparasite. Nevertheless, such a 3-way linkage remains to be demonstrated.

In an attempt to unravel the evolution of the fungal symbioses of bryophytes, Pressel *et al*. (2010) examined the ancient basal bryophytes ***Treubia*** (Figure 110-Figure 111) and ***Haplomitrium*** (Figure 116-Figure 117. In these liverworts they found intracellular fungal lumps, inter cellular hyphae, and thick-walled spores. Unlike the well known glomerophytes found as symbionts in thallose liverworts and lower tracheophytes, these were more ancient fungi (Figure 130-Figure 131).

In leafy liverwort families sister to the **Schistochilaceae**, the ascomycete fungus ***Rhizoscyphus ericae*** occurs in the rhizoids (Pressel *et al*. 2010). This fungus has a wide range of hosts, including flowering plants in the Ericales (includes blueberries and heath

plants) and an Antarctic species of the leafy liverwort ***Cephaloziella***. Figure 132 shows a member of the **Ascomycota** inhabiting ***Mylia anomala***. In the **Basidiomycota**, the genus ***Sebacina*** (Figure 133) is associated with leafy liverworts, but this fungus is host specific. Neither of these liverwort fungi seems to digest its host, whereas the **Basidiomycota** in the thallose liverworts of **Aneuraceae** have regular colonization and digestion cycles. The hornworts also demonstrate mycorrhizal relationships with fungi, but thus far there is no evidence that such a mycorrhizal relationship exists in mosses.

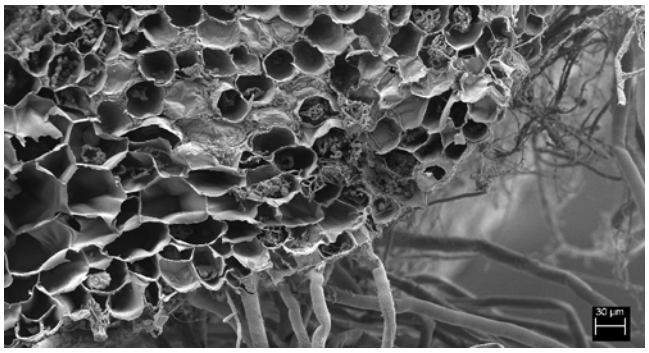

Figure 130. SEM of ***Treubia*** cross section showing the number of cells with resident fungi. Photo courtesy of Jeff Duckett and Silvia Pressel.

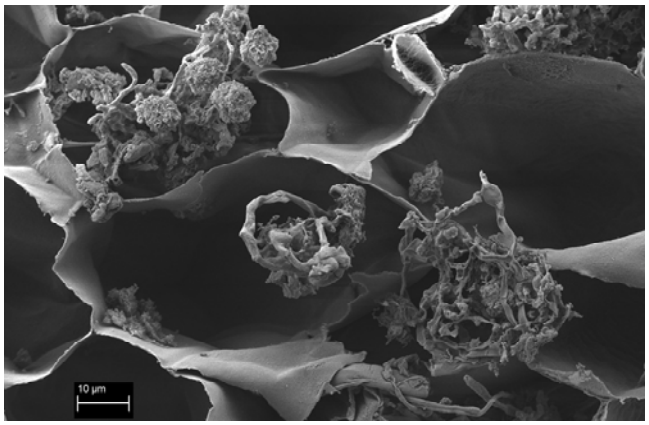

Figure 131. SEM of ***Treubia*** cross section with fungi in cells. Photo courtesy of Jeff Duckett and Silvia Pressel.

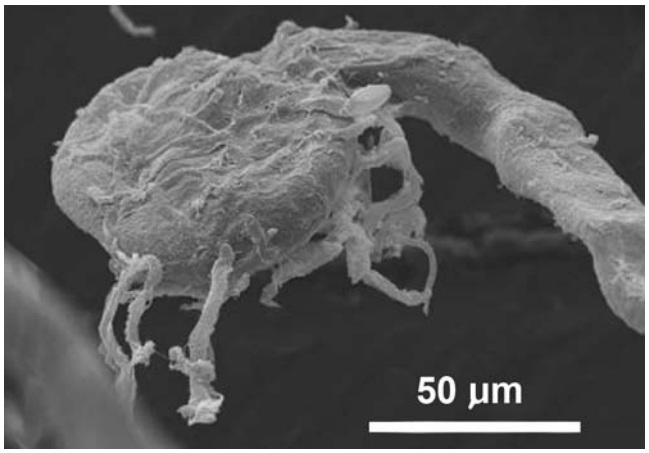

Figure 132. Swollen rhizoid tip with Ascomycota in leafy liverwort ***Mylia anomala***. Photo courtesy of Silvia Pressel and Jeff Duckett.

Figure 133. ***Sebacina incrustans***, member of a genus of basidiomycete fungi that is associated with leafy liverworts. Photo by James K. Lindsey, with permission.

We are at a very early stage in our understanding of mycorrhizae in bryophytes. In tracheophytes these associations permit the host plant to gain water and nutrients from a much wider area by accepting these from a fungus that has grown over a wide area, as much as 15 hectares, weighing 10,000 kg (Smith *et al*. 1992). Their role in bryophytes is less clear, but the ancient origin of this association suggests that by now it could be quite sophisticated and beneficial.

Protonema

The protonema stage of mosses is a delicate threadlike stage in which every cell is surrounded by air with the potential for creating desiccation. But is it really so delicate?

In experiments, Pressel and Duckett (2010) demonstrated that protonemata can survive slow drying but not fast drying. This suggests that during slow drying there is time to manufacture something that protects the cells from the effects of desiccation. Indeed, pre-treatment with abscisic acid permits the protonemata to survive fast drying as well. During slow dehydration the cells undergo profound changes, including vacuolar fragmentation, reorganization of endomembrane domains, changes in cell wall thickness, changes in plastid morphology, changes in mitochondria morphology, and a controlled dismantling of the cytoskeleton. During fast drying, these events do not occur or are incomplete. The abscisic acid permits the rapidly drying cells to partially mimic their behavior during slow drying, permitting them to survive.

Leafy Liverwort Gemmae

Liverworts have leaf gemmae that are usually small structures along the leaf margins. Germination on the leaf is not desirable, so it is no surprise that they have a means of preventing it. This prevention may relate to their hydrophobic surface (Duckett & Ligrone 1995). In ***Odontoschisma denudatum*** (Figure 134), the wall chemistry changes during maturation, with an increase in electron-opacity.

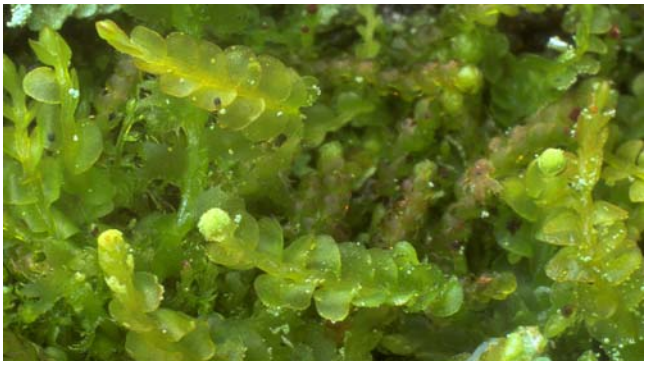

Figure 134. ***Odontoschisma denudatum*** with gemmae on apical leaves (yellowish). Photo by Jan-Peter Frahm, with permission.

Sporophyte

When we examine mature sporophytes with their capsules and spores, we don't give a second thought to the dangers of drying out. But we are misled by this resistant mature sporophyte. Rather, based on studies of field-collected gametophytes of ***Microbryum starckeanum*** (Figure 135) and ***Tortula inermis*** (Figure 136) (both species of dry habitats) with immature sporophytes, McLetchie and coworkers found that the sporophyte generation is more sensitive to desiccation and thermal stress than is the leafy gametophyte (McLetchie & Stark 2006; Stark *et al*. 2007). This may of course differ in species with a different phenology in different environmental conditions, but it bears questioning our perception of the importance of desiccation during sporophyte development. This need for desiccation tolerance of the sporophyte may be especially important for species like those of ***Polytrichum*** that require as much as 20 months for sporophyte development and span an entire year of weather conditions (Arnell 1905; Longton 1972).

Figure 135. ***Microbryum starckeanum***, a species in which the sporophyte is more sensitive to desiccation than the gametophyte. Photo from BBS website, with permission.

It appears that the embryonic sporophytes are the stage most susceptible to desiccation stress (Stark 2002, 2005). Nevertheless, some desert mosses have embryonic sporophytes that can tolerate desiccation for long periods, most likely benefitting from **desiccation hardening** (development of resistance to desiccation) (Stark *et al*. 2014). Several examples exist from non-desert mosses, although the tie to desiccation is unclear. In the boreal forest moss ***Hylocomium splendens*** (Figure 126-Figure 127) (Callaghan *et al*. 1978) and desert moss ***Syntrichia caninervis*** (Figure 18) (Stark *et al*. 2000), the number of aborted sporophytes outnumbers that of mature sporophytes. Similarly, in the boreal forest moss ***Pleurozium schreberi*** (Figure 137) 38% of the sporophytes aborted (Longton & Greene 1969).

Figure 136. ***Tortula inermis*** leaves and immature capsules, a species in which the young capsules are more sensitive to desiccation that the gametophytes. Photo by Michael Lüth, with permission.

Figure 137. ***Pleurozium schreberi***, a boreal forest moss with a high percent of abortions. Photo by Michael Lüth, with permission.

Calyptra Protection

If we imagine the hairy calyptrae of such mosses as ***Polytrichum*** (Figure 138), we must ask ourselves how the calyptra avoids absorbing water and holding it against the capsule, creating water logging, or contrarily, draws water from the capsule due to capillary spaces created by the hairs. In other words, why doesn't it behave like a bath towel? To answer this question, we will look at calyptra development, timing, structure, and its ultimate role.

Figure 138. Hairy calyptra on capsule of ***Polytrichum juniperinum***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

The **calyptra** develops from the archegonium, which expands as the embryo develops. In some cases, the calyptra falls early in capsule expansion, but in others, such as ***Polytrichum***, it may remain until the spores are shed. One might then question the role of the calyptra in protecting the embryo through to development of spores. Budke *et al.* (2012) demonstrated that the maternal calyptra provides protection of early post-embryonic sporophytes against desiccation, but that later development of the capsule may incur cuticle development that protects as the capsule emerges from the calyptra. This demonstrates that the calyptra cannot be considered a vestigial structure, but rather that it is essential in preventing desiccation. Haig (2013) agrees that the presence of the calyptra delays the onset of transpiration. Hence, it is prudent to examine the calyptra characters that may provide this desiccation protection.

Cuticle: We have already discussed the presence of a 4-layered cuticle for the duration of the calyptra in ***Funaria hygrometrica***. Budke *et al*. (2011, 2012, 2013) demonstrated that the cuticle on this calyptra conferred significant protection to the developing sporophyte.

Hairs: There appear to be two kinds of hairs on calyptrae, "true" hairs and undeveloped archegonia. In ***Fontinalis***, the calyptral hairs develop from aborted archegonia whose eggs (Figure 139) were presumably not fertilized (Glime unpubl.). This results in a small number of hairs near the base of the calyptra.

The hairs on the calyptrae in taxa such as ***Polytrichum*** (Figure 138) and ***Orthotrichum*** (Figure 140) could function to prevent desiccation during early development or to deter herbivory both early and late in development, but earlier in development they could also serve important functions for the archegonium, helping to conserve moisture to protect the egg or other uses we haven't considered. I haven't followed the development in taxa other than ***Fontinalis*** (Figure 139), but the hairs seem too large and numerous in most taxa to be just a lingering of the archegonia or associated paraphyses. If they continue to elongate as the calyptra develops, then there may be some advantage that would favor that prolonged use of energy for their development.

Cuticle

It is likely that many bryophyte sporophytes have a **cuticle**. For example, the large, waxy-looking capsule of ***Buxbaumia viridis*** (Figure 141), and most likely the other members of the genus, has a layered cuticle (Koch *et al.* 2009). And in ***B. viridis*** this cuticle is waxy with massive wax layers having small embedded and superimposed platelets and granules on top of this complex. Although until recently the only documented sporophyte cuticles had been those of the **Polytrichales**, this complex of cuticle components is common in various groups of tracheophytes.

Pressel and Duckett (2011), suspecting that capsule waxes were more common than those of these two groups, examined a wider array of taxa, particularly those with shiny surfaces. They demonstrated that ***Bartramia*** (Figure 142), ***Plagiopus*** (Figure 143-Figure 144), and ***Mnium*** (Figure 145-Figure 147) invested as much in surface waxes of the capsule as did ***Polytrichum***. They interpreted these waxes as having a role in preventing accumulated water from depressing gas exchange in the capsules, that is, prevention of water logging.

Figure 139. ***Fontinalis squamosa*** calyptra with young archegonium SEM. Photo by Janice Glime.

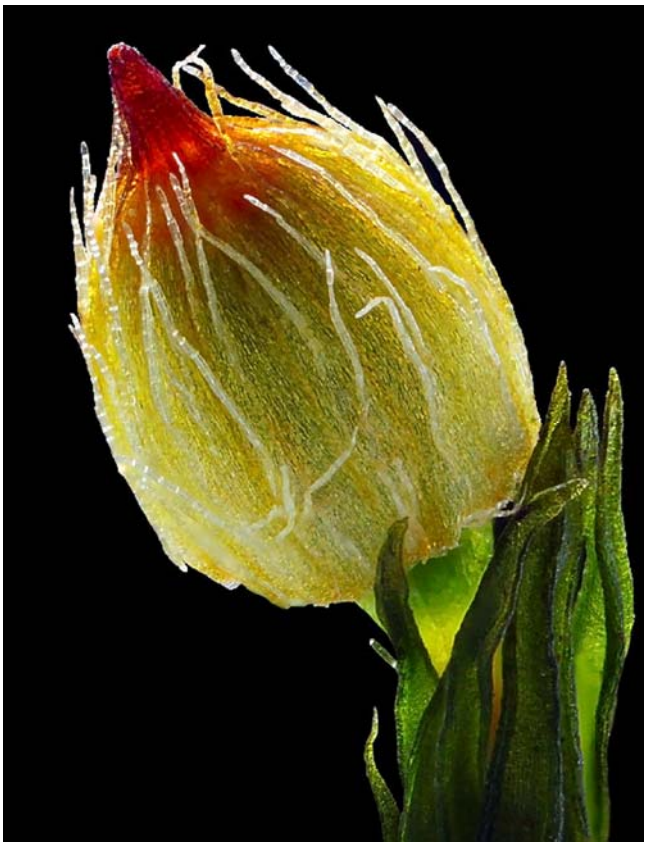

Figure 140. ***Orthotrichum stramineum*** with calyptra showing long hairs. Photo by Des Callaghan, with permission.

Figure 141. ***Buxbaumia viridis*** capsule showing shiny, waxy cuticle. Photo by Bernd Haynold, through Wikimedia Commons.

Figure 142. ***Bartramia pomiformis*** capsule showing waxy surface. Photo by Walter Obermayer, with permission.

Figure 143. ***Plagiopus oederiana*** with capsules showing waxy surface. Photo by Michael Lüth, with permission.

Figure 144. ***Plagiopus oederiana*** waxy capsule with calyptra at near maturity. In this case, the calyptra does little to protect the nearly mature capsule, most likely making the cuticle more important. Photo by Janice Glime.

Figure 145. ***Mnium*** sp. with water on young capsules, illustrating the potential for water logging. Photo by Alan S. Heilman, through Creative Commons.

In ***Orthotrichum*** many species have immersed stomata (Figure 146). These openings are surrounded by protruding cells that maintain an air space between the capsules and the calyptra (which remains attached and covers most of the capsule until the spores are ripe; Figure 140) (Pressel & Duckett 2011). The waxes repel the water on the capsule and prevent it from being drawn under the calyptra by capillary action. That is, a primary role for these surface waxes may be to prevent water logging in this and other species.

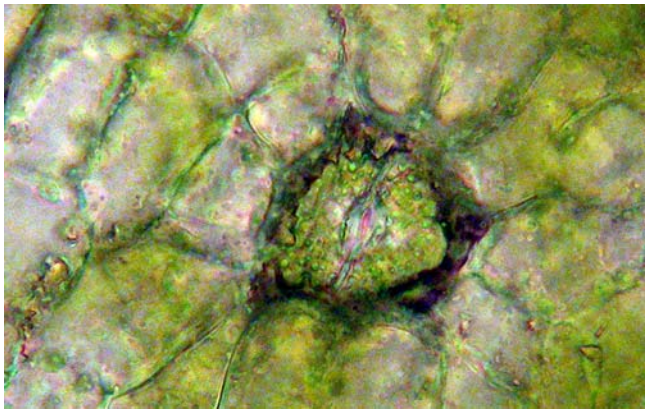

Figure 146. ***Orthotrichum pusillum*** immersed stoma on calyptra. Photo by Bob Klips, with permission.

Figure 147. ***Mnium hornum*** with capsule showing waxy surface. Photo by J. C. Schou, with permission.

But this cuticle story apparently does not begin with the capsule. The young sporophyte is covered by a calyptra. And in ***Funaria hygrometrica*** (Figure 148-Figure 151) this calyptra is covered by a waxy cuticle four layers thick at all stages, hence providing protection long before the developing sporophyte develops its own cuticle that ultimately arises on the sporangium (Budke *et al*. 2012). When the calyptra cuticle is removed during periods of low moisture, the sporophyte suffers significant damage, including decreased survival, increased tissue damage, incomplete sporophyte development, more peristome malformations, and decreased reproductive output (Budke *et al*. 2013). This is in contrast to the conclusion of Pressel and Duckett (2011) that the cuticles function primarily to prevent water logging. I have for my entire career as an ecologist failed to understand why ecologists get into so many arguments over two or more different explanations for the same thing, in this case the presence of stomata. There seems to me to be no evolutionary argument against multiple functions for the same thing, at the same or at different times. Just consider the many functions of our brains, or the many uses for fingernails.

Budke *et al*. (2012) examined the development of the cuticle on both the calyptra and the capsule, using ***Funaria hygrometrica*** (Figure 148-Figure 151) as a model organism. These researchers found that the sporophyte cuticle does not mature until the formation of the capsule.

Figure 148. ***Funaria hygrometrica*** with expanding archegonia (now calyptrae) with young sporophytes still mostly protected within the perichaetial leaves. Photo by Andrew Spink, with permission.

Figure 149. ***Funaria hygrometrica*** young sporophytes and calyptrae emerging from the protection of the perichaetial leaves. Photo by Michael Lüth, with permission.

Figure 150. ***Funaria hygrometrica*** mature capsules that have lost the calyptrae. Photo by Robert Klips, with permission.

Figure 151. ***Funaria hygrometrica*** mature capsule showing waxy surface. Photo by Sarah Gregg, with permission.

As among leaves, the capsule waxes vary in structure. In ***Tetradontium brownianum*** (Figure 152), there are fine rods around the stomata, whereas in ***Pylaisia polyantha*** (Figure 153) there are both rods and fine whorls (Pressel & Duckett 2011).

Figure 152. ***Tetradontium brownianum***, a species with fine rods in the cuticle around the stomata of the capsules. Photo by Michael Lüth, with permission.

Figure 153. ***Pylaisia polyantha*** capsule, a species with both rods and fine whorls in the cuticle around the stomata. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Peristome: Peristome teeth likewise have cuticles, with differences related to habitat conditions at the time of spore discharge (Pressel & Duckett 2011). In **Polytrichales**, the spores are dispersed when raindrops pounce on the diaphragm (**epiphragm;** Figure 154) that connects the teeth (Watson 1971). For this mechanism to work, the teeth must not only remain dry, but must repel water so that it does not block the small openings between the teeth where spores must exit (Pressel & Duckett 2011).

Figure 154. Top view of ***Polytrichum*** epiphragm showing the 64 adherent teeth. Water splashing on the membranous epiphragm (like a child on a trampoline) disperses the spores. Photo by George Shepherd, through Creative Commons.

On the other hand, most mosses disperse their spores when it is dry. Water is taken up and lost rapidly from between the ornamentation on these peristomes (Pressel & Duckett 2011). These include all **Bryopsida** they tested: ***Amblystegium*** (Figure 155), ***Bryum*** (Figure 102), ***Coscinodon*** (Figure 156), ***Dicranella*** (Figure 157), ***Didymodon*** (Figure 158), ***Fissidens*** (Figure 159), ***Funaria*** (Figure 160), ***Grimmia*** (Figure 80), ***Hypnum*** (Figure 161), ***Mnium*** (Figure 145-Figure 147), ***Rhynchostegium*** (Figure 162), ***Schistidium*** (Figure 75), ***Syntrichia*** (Figure 18), ***Tortula*** (Figure 1, Figure 136). These water gains and losses permit rapid closure in wet conditions and accelerate opening under dry conditions.

Figure 155. ***Amblystegium serpens*** capsules. Photo by Michael Lüth, with permission.

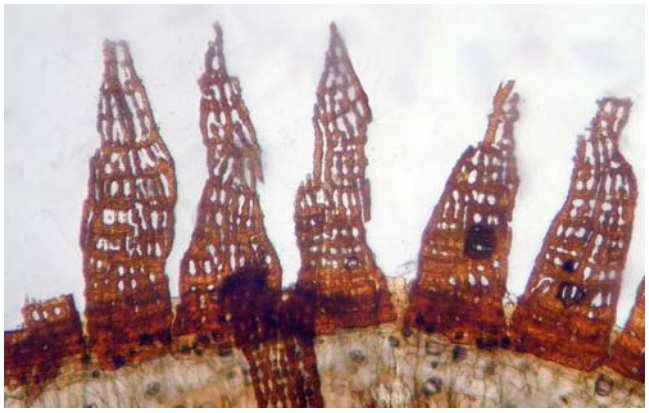

Figure 156. ***Coscinodon cribrosus*** peristome. Photo by Michael Lüth, with permission.

Figure 157. ***Dicranella varia*** capsules showing peristome. Photo by Kristian Peters, through Wikimedia Commons.

Figure 158. ***Didymodon rigidulus*** with capsules. Photo by Michael Lüth, with permission.

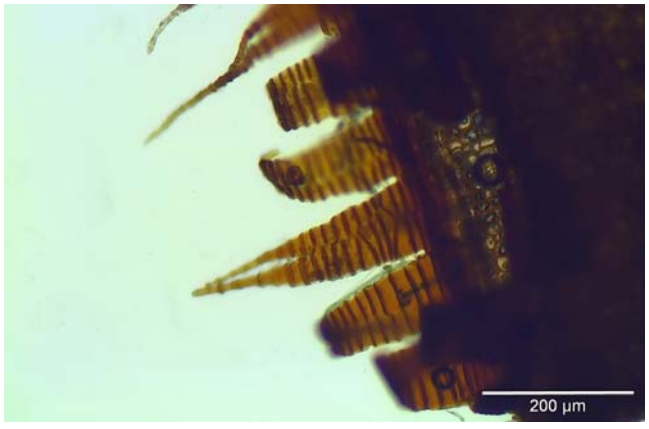

Figure 159. ***Fissidens adianthoides*** peristome. Photo by Kristian Peters, with permission.

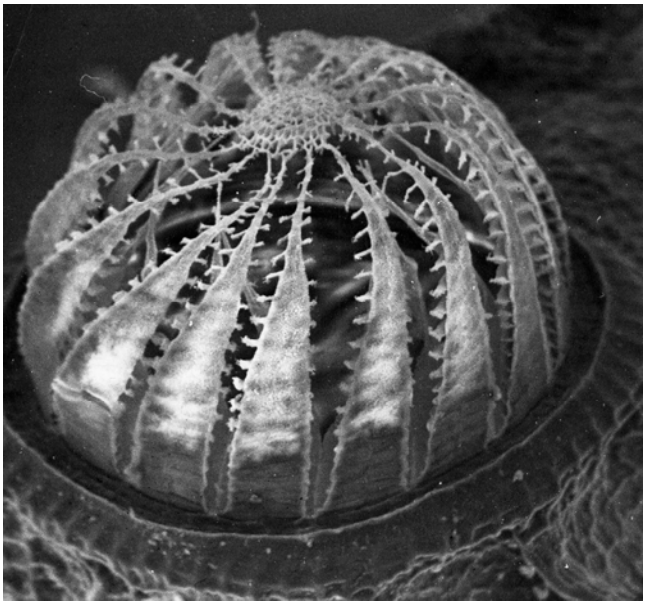

Figure 160. Peristome teeth of ***Funaria hygrometrica***, a species in which teeth move in response to drying conditions and spores escape from the spaces between the teeth. Photo by George Shepherd, through Creative Commons.

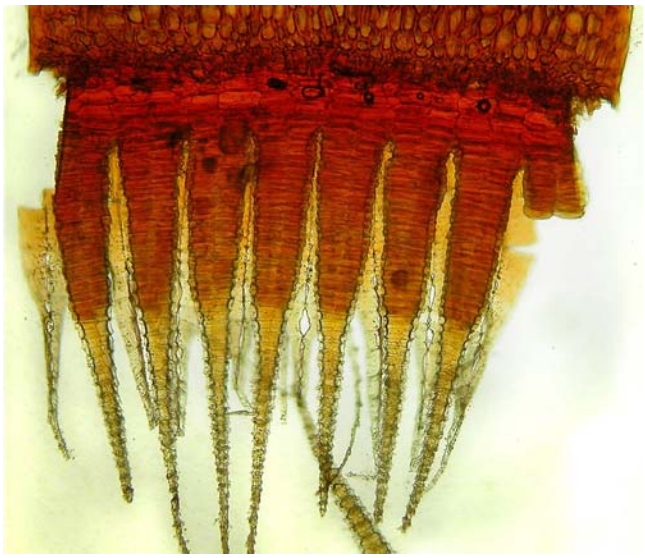

Figure 161. ***Hypnum cupressiforme*** peristome. Photo by Walter Obermayer, with permission.

Figure 162. ***Rhynchostegium confertum*** with capsules. Photo by Michael Lüth, with permission.

But what happens in capsules with no teeth or only rudimentary peristomes? As an example, in ***Weissia*** (Figure 163) water is prevented from entering the capsule by a highly water-repellent capsule rim (Figure 163). If water entered the capsule, it could cause premature germination or interfere with ultimate dispersal.

Figure 163. ***Weissia fallax*** capsule showing rudimentary peristome. Note the waxy appearance of the reddish annulus around the teeth. Photo by Michael Lüth, with permission.

Guard Cells and Stomata

Capsules of many (most?) mosses have guard cells and stomata. The guard cells usually resemble those of tracheophytes, having a doughnut shape, and surrounding the **stoma** (opening). These are mostly located at the base of the capsule. In addition to the cuticle, we might expect the **guard cells** to play a role in water relations of the capsule. After all, the stomata and guard cells have existed through 400 million years of land plant evolution (Chater *et al*. 2011).

Like the cuticle, the role of the pores and stomata has been overlooked in bryophytes. Although we have known about the stomata in moss capsules for a long time, and used them as taxonomic characters in genera such as ***Orthotrichum***, we have largely ignored their function, failing even to ask what it might be.

When thinking about adaptations to drought, we usually think of the survival of the gametophyte. What danger could there be to a dry capsule full of spores, right? But before that capsule is full of spores, it is a photosynthetic body in need of water. Perhaps the young seta with no capsule has little problem, but once the capsule starts to differentiate, water needs most likely increase dramatically. And once meiosis begins, water needs are critical. An interruption during meiosis could lead to a variety of anomalies, many of which could cause spore death.

Paton and Pearce (1957) reviewed the early literature on stomata in bryophytes, pointing out that in ***Sphagnum*** they do not mature. In fact, the capsule pores of ***Sphagnum*** are considered **pseudostomata**. Their function seems to be limited, facilitating capsule dehydration, shape change, and dehiscence (Duckett *et al*. 2009; Merced 2015). This is not surprising, because in ***Sphagnum***, the seta is only a few cells high. Instead, the capsule is elevated on a **pseudopodium** that is developed from the gametophyte. This pseudopodium does not extend until the capsule is mature. Hence, the role of the pseudostomata to create a transpiration stream for nutrient transport would seem futile. Rather, Duckett and coworkers (2009) provide evidence that the pseudostomata remain open when the capsule is mature, causing the capsule to dry and shrink, forcing the spores out.

Stomata also are absent in the liverworts (thallus pores excepted), present in at least some hornworts, and absent in the moss order **Andreaeales** (Figure 164-Figure 165) (Paton & Pearce 1957). As in the tracheophytes, the number of guard cells associated with a stoma is usually two. Known exceptions (single circular guard cells) occur in **Funariaceae** (Figure 148-Figure 151) and ***Buxbaumia aphylla*** (Figure 166). Larger numbers of guard cells (3-4) occur but do not seem to be consistent in any single taxon and are thus considered an anomaly.

The walls of the guard cells are strongly cuticularized (Paton & Pearce 1957). The number of stomata in capsules that have been examined varies from 4 to over 200. Species with a long seta generally have more stomata than species with a short seta or immersed capsules. This supports the hypothesis that they are needed to provide an adequate transpiration stream to transport nutrients from the leafy gametophyte to the sporophyte capsule (Haig 2013).

Figure 164. ***Andreaea rothii*** with capsules that have no stomata. Photo by Jan-Peter Frahm, with permission.

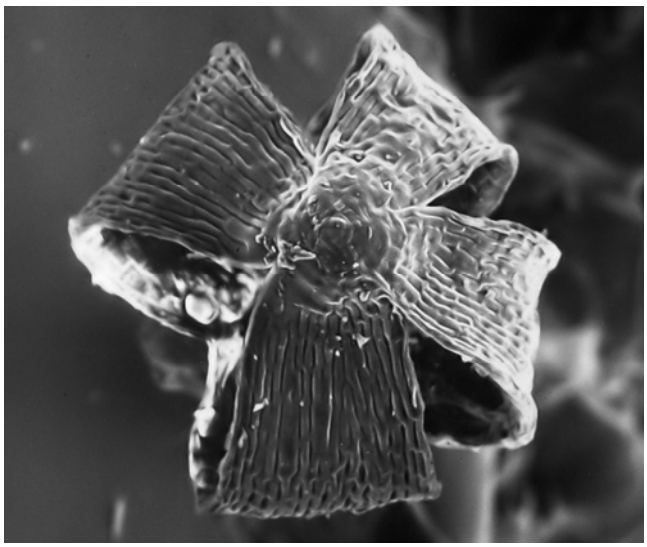

Figure 165. ***Andreaea*** capsule SEM, a capsule that lacks stomata. Photo by George Shepherd, through Creative Commons.

Guard cells are usually located at the base of the capsule. In reality, they tend to be located below the area covered by the calyptra, where gas exchange and water loss are possible. This is consistent with a role to permit water loss, but could they also serve in gas exchange? It appeared that the capsule guard cells did not respond to changes in humidity (Copeland (1902). Rather, they are only able to close when the sporophyte is dehydrated or reopen when it is remoistened. This is consistent with their potential role in bringing nutrients upward.

In the moss ***Physcomitrella patens*** (Figure 167-Figure 168), the stomata of the sporophytes do indeed respond to environmental signals with the hormone abscisic acid (ABA) serving as a signalling component. In fact, the genes controlling ABA in ***P. patens*** can be moved to mutant ***Arabidopsis thaliana*** (flowering plant) that has lost its ABA-regulatory gene and cause stomata in that plant to behave normally. When ***P. patens*** mutants lack the ABA regulatory gene, the response to ABA is greatly reduced.

Figure 166. ***Buxbaumia aphylla*** capsules, a species with single circular guard cells. Photo by Štěpán Koval, with permission.

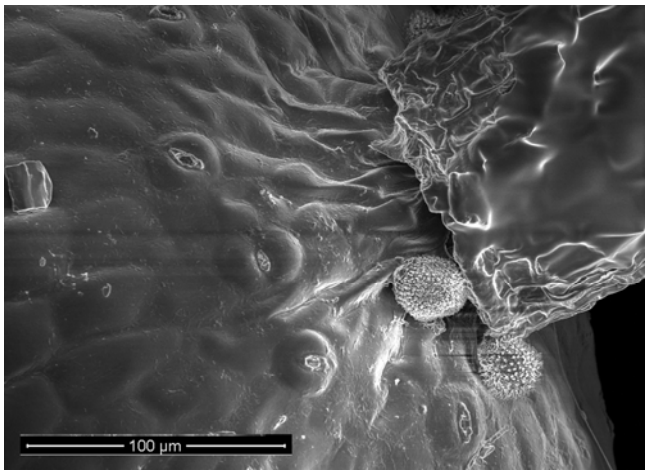

Figure 167. ***Physcomitrella patens*** capsule stomata SEM. Photo courtesy of Jeff Duckett and Silvia Pressel.

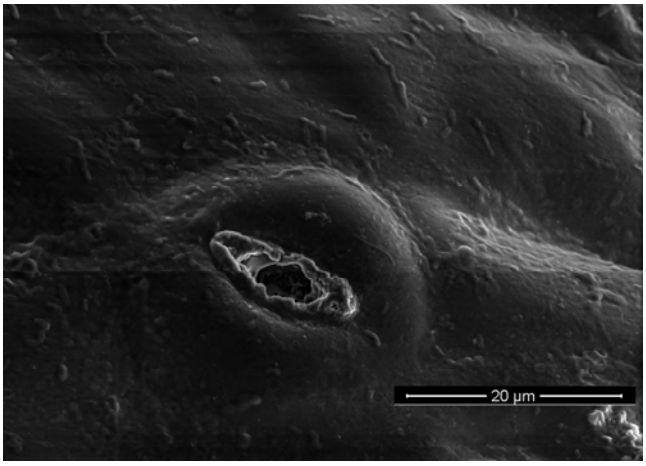

Figure 168. SEM of ***Physcomitrella patens*** stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.

But wait! While ABA may affect guard cell closure in ***Physcomitrella patens*** (Figure 168), it appears that the guard cells in mosses have a somewhat different function. First of all, there seems to be no potassium-regulating mechanism (Duckett *et al*. 2010a). Instead, their primary role seems to be to permit water to escape when the capsule is mature (Boudier 1988; Beerling & Franks 2009; Duckett *et al*. 2009, 2010b). This loss of water causes the capsule to become distorted enough to force the rather stiff circular cap (**operculum**) to pop off.

It appears that the stomata endow the capsule with multiple advantages. Loss of water during development could be important to create a transpiration stream that moves nutrients upward from the gametophyte to the capsule of the sporophyte (Haig 2013). If this interpretation is correct, the water loss is essential to maintain continuous movement of water and associated nutrients upward. In fact, Haig interprets the elevation of the capsule on an elongated seta to be an adaptation that increases the movement of water by placing the capsule into the zone of turbulent air above the quiet boundary layer. The placement of the stomata at the base of the capsule gives them exposure while the calyptra reduces water loss from the part of the capsule where spores are developing.

Ziegler (1987) pointed out that in some mosses the sporophyte guard cells have thick walls and do not open and close. This type of guard cell occurs in species that have reduced photosynthetic tissue in the capsule and have been considered evolutionarily reduced. Bryophyte guard cells also differ from those of tracheophytes in that they are larger than the surrounding cells, whereas in tracheophytes they are smaller.

Paton and Pearce (1957) found that the stomata become functionless at a relatively early stage in capsule development, suggesting that this loss in function protects the developing spores against desiccation. They were able to demonstrate this early loss of function in the hornwort ***Anthoceros*** (Figure 169-Figure 170) and in mosses in the **Bryales**. Based on their studies on the hornwort ***Phaeoceros***, Duckett and Ligrone (2003) say no to the function of capsule guard cells in gas exchange, at least in hornworts; they could find no response to moisture changes or to ABA in the hornwort ***Phaeoceros*** stomata (Figure 171).

Figure 169. ***Anthoceros agrestis*** with capsules. Photo by Michael Lüth, with permission.

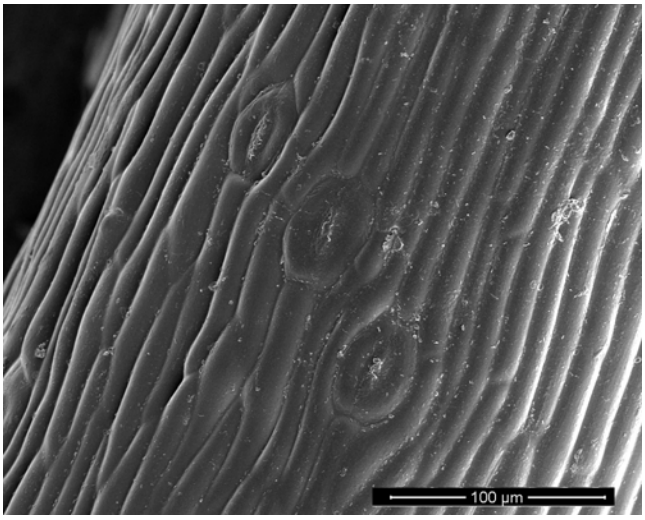

Figure 170. ***Anthoceros punctatus*** SEM image of sporophyte showing stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.

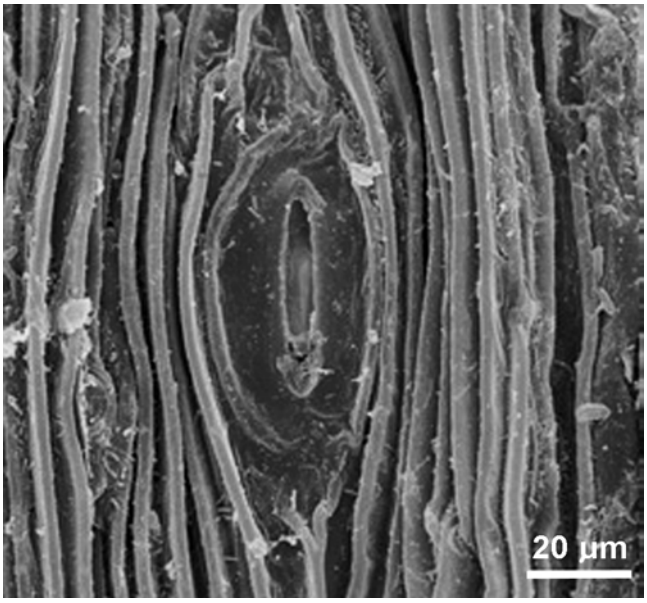

Figure 171. ***Phaeoceros laevis***, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo courtesy of Jeff Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel.

On the other hand, in greenhouse-grown ***Funaria hygrometrica*** (Figure 172) the stomata (Figure 173) open on the fourth day of capsule expansion (Garner & Paolillo 1973). By the fifth day, continuing through the tenth day, they close in darkness and reopen in light. They also can be closed by the application of abscisic acid (ABA) (Garner & Paolillo 1973; Chater *et al*. 2011). Thus far we have no evidence to demonstrate the usefulness of this opening and closing. It could enhance gas exchange; it could control water loss during the critical stages of meiosis; and it could serve as a transpiration stream to bring nutrients from the gametophyte. And the function could change or disappear at maturity.

Figure 172. ***Funaria hygrometrica*** capsules. Photo by Li Zhang, with permission.

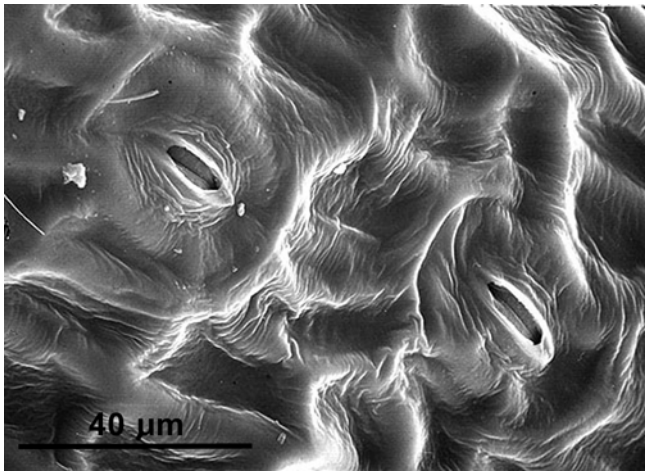

Figure 173. ***Funaria hygrometrica*** stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.

Indeed it appears that the function changes as the ***Funaria hygrometrica*** (Figure 172-Figure 173) capsule ripens. As maturity approaches, the stomatal responsiveness declines and about half the stomata remain open day and night (Garner & Paolillo 1973)! Furthermore, more stomata become exposed when the calyptra is shed (Duckett *et al*. 2009, 2010a). The stomata no longer provide a mechanism to conserve water.

Further complicating our interpretation of stomatal function during capsule development is the apparent lack of relationship between the presence of stomata and habitat. In the liverworts, stomata are totally absent. But liverworts produce mature capsules before elongation of the stalk occurs, negating the necessity for long distance

translocation of nutrients and being consistent with the observations of Paton and Pearce (1957) that fewer stomata occurred on moss capsules with short or absent setae than on those with emergent, longer setae. The widespread absence of stomata in at least some species among so many moss taxa [*e.g.* ***Atrichum*** (Figure 174), ***Pogonatum*** (Figure 175), ***Acaulon*** (Figure 176), ***Campylopus*** (Figure 177), ***Leucobryum*** (Figure 178), ***Cinclidotus*** (Figure 179), ***Discelium*** (Figure 180), ***Nanomitrium***, ***Fontinalis*** (Figure 183), ***Tetraphis*** (Figure 182), ***Catoscopium***, ***Leucodon***, ***Cyclodictyon***) (Paton & Pearce 1957)] suggests they are not essential for gas exchange. Furthermore, since most of these genera have long setae, one could argue against their function in creating a transpiration stream for nutrient transport. One might also argue that the well developed vascular tissue in both gametophytes and sporophyte setae of the **Polytrichaceae** makes the presence of stomata to create a transpiration stream unnecessary for nutrient transport, yet some members of the family have stomata and guard cells. And the stomata in tracheophytes are certainly necessary to maintain function of the xylem tissue in these larger plants.

Figure 174. ***Atrichum crispulum*** capsules – in a genus in which at least some species lack stomata. Photo by Robert Klips, with permission.

Figure 175. ***Pogonatum urnigerum*** capsules, member of a genus in which some species lack stomata. Photo by Kristian Peters, with permission.

Figure 176. ***Acaulon muticum*** with capsules, a genus in which species lack stomata. Photo by Michael Lüth, with permission.

Figure 177. ***Campylopus nivalis*** capsules, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 178. ***Leucobryum glaucum*** with capsules, member of a genus in which capsules often lack stomata. Photo by Janice Glime.

Figure 179. ***Cinclidotus fontinaloides***, a species that lacks stomata. Photo by Michael Lüth, with permission.

Figure 180. ***Discelium nudum*** capsule, a genus in which at least some members lack stomata. Photo by Des Callaghan, with permission.

Figure 181. ***Catoscopium nigritum***, a genus with capsules that lack stomata. Photo by Michael Lüth, with permission.

Figure 182. ***Tetraphis pellucida*** capsule, a genus that lacks stomata. Photo by Walter Obermayer, with permission.

Figure 183. ***Fontinalis squamosa*** var ***curnowii*** with capsules, a species that lacks stomata. Photo by David Holyoak, with permission.

Merced and Renzaglia (2013) demonstrated the remarkable similarity between stomata in the highly developed ***Oedipodium*** (Figure 184) and the very reduced ***Ephemerum*** (Figure 185) capsules. The capsule structure differs, with ***Oedipodium*** having extensive spongy tissue along the capsule apophysis where stomata are concentrated and ***Ephemerum*** lacks such tissue but has minimal substomatal cavities. Although ***Oedipodium*** (Figure 184) has numerous long-pored stomata and ***Ephemerum*** has few round-pored stomata, the stomatal ultrastructure and wall thickenings of these two taxa are quite similar. Both have sporophytes with a cuticle that is thicker on the guard cells and extends on the walls surrounding the stomata. When the capsules are older, epicuticular waxes and pectin clog the pores, closing them much like the stomata of fir trees in winter. Merced and

Renzaglia argue that the cuticle, water-conducting cells, and spongy tissues of ***Oedipodium*** all support the role of stomata in facilitating gas exchange and water transport as the sporophyte develops. They also contend that the existence of stomata exclusively on capsules may indicate a function in drying and dispersal of spores.

Figure 184. ***Oedipodium griffithianum*** with young capsules, a species with a well developed spongy apophysis and many stomata. Photo by Des Callaghan, with permission.

Figure 185. ***Ephemerum recurvifolium*** with capsules, a moss that lacks a spongy apophysis and has few stomata. Photo by Tomas Hallingback, with permission.

Hence, we have four potential functions for the stomata of capsules. These include a role in creating a transpiration stream to aid in nutrient transport, prevention of water logging that inhibits gas exchange, regulation of gas exchange, and drying that contracts the capsule and aids in spore expulsion.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. When fully hydrated, their water content is typically high, up to more than 1200% of their dry mass. When dry, they can survive months to many years. Structural adaptations of stems and whole plants such as **growth form**, **branch** and **leaf arrangements**, **rhizoidal tomentum**, **mucilage**, **central strand**, **hydroids**, **paraphyllia**, **ventral scales, cuticles**, and **stomata** aid in moving water, facilitating entry, or reducing loss.

Thallose liverworts benefit from ventral transport by rhizoids and scales. The dorsal surface is covered by a cuticle but gas exchange may occur through pores overlying photosynthetic chambers. The pores are ringed by cells with cuticular ridges that prevent water drops from entering but that allow water vapor to escape. Midribs may help to gather and direct water both externally and internally. For many taxa, dormancy is a "last resort" to avoid the effects of desiccation. Fungal partners occur in both thallose and leafy liverworts, but their role is not known. Smooth rhizoids facilitate fungal entry; pegged rhizoids transport water and the pegs prevent collapse upon drying.

In mosses and leafy liverworts, growth form can help in both movement and conservation of water. Clumps reduce transpiration and provide additional capillary spaces. Mixed species can help each other, especially if one is good at moving water and one is good at retaining it. Mosses may have a central strand where water moves, but this is apparently absent in all liverworts except the **Haplomitriopsida**. Leaf cuticles occur in both mosses and liverworts and may repel water to avoid water logging or reduce loss by transpiration. **Rhizoids** and **tomentum** help in the movement of water upward. **Mucilage** in some liverworts, especially **Haplomitriopsida**, can be of great value in holding water about the plants.

The protonema can usually withstand slow drying. Like the guard cells in some stomata, it is responsive to **ABA**. ABA may be linked to **inducible desiccation tolerance** in the gametophores. **Constitutive desiccation tolerance** is the most common form of desiccation tolerance in bryophytes, but as the plants age they may switch to inducible desiccation tolerance. **Hardening** can occur following slow drying and may last more than a few days.

The sporophyte and calyptra both have **cuticles**, and at least in ***Funaria hygrometrica***, the cuticle in the calyptra matures first, helping the calyptra to protect the young embryo. Calyptra hairs, thallus hairs,

paraphyllia, and paraphyses all function to help in movement of water and reduce rate of drying. Capillary spaces provided by these can further facilitate absorbing and holding water, bathing the tissues in water and reducing water loss.

The sporophytes of most(?) mosses and hornworts have **guard cells** and **stomata** that cease to function at sporophyte maturity. Their function(s) are ambiguous, but they may contribute to creating a transpiration stream to move nutrients upward, regulating capsule hydration during development, and drying the capsule prior to dehiscence and dispersal.

Acknowledgments

An earlier version of this chapter benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me explain things without leaving too much to one's imagination, but at the same time not repeating myself. In an earlier version Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective.

Literature Cited

Alpert, P. 1979. Desiccation of desert mosses following a summer rainstorm. Bryologist 82: 65-71.

Alpert, P. 1982. Poikilohydry and desiccation tolerance in some xerophytic mosses. Ph. D. Dissertation, Harvard University, Cambridge, pp. 19-31.

Alpert, P. 1985. Distribution quantified by microtopography in an assemblage of saxicolous mosses. Vegetatio 64: 131-139.

Alpert, P. 2000. The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol. 151: 5-17.

Alpert, P. and Oechel, W. A. 1985. Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. Ecology 66: 660-669.

Alpert, P. and Oechel, W. C. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. Amer. J. Bot. 74: 1787-1796.

Alpert, P. and Oliver, M. J. 2002. Drying without dying. In: Black, M. and Pritchard, H. W. (eds.). Desiccation and survival in plants: Drying without dying. CABI Publishing, Wallingford, pp. 3-43.

Arnell, H. W. 1905. Phaenological observations on mosses. Bryologist 8: 41-44.

Atala, C. and Alfaro, J. F. 2012. Vascular architecture of the dendroid antipodean moss *Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. (Polytrichaceae). J. Bryol. 34: 277-280.

Bates, J. W. 1989. Retention of added K, Ca and P by *Pseudoscleropodium purum* growing under an oak canopy. J. Bryol. 15: 589-605.

Bates, J. W. 1998. Is 'life-form' a useful concept in bryophyte ecology? Oikos 82: 223-237.

Bayfield, N. G. 1973. Notes on water relations of *Polytrichum commune* Hedw. J. Bryol. 7: 607-617.

Beerling, D. J. and Franks, P. J. 2009. Evolution of stomatal function in 'lower' land plants. New Phytol. 183: 921-925.

Berthier, J., Bonnot, E.-J., Fabre, M.-C, and Hébant, C. 1974. L'appare sécréteur des Bryales: Données morphologiques, ultrastructurales et cytochimiques. Bull. Soc. Bot. France 121(Suppl. Coll. Bryol.): 97-100.

Best, A. C. 1950. The size distribution of raindrops. Quart. J. Royal Meteorol. Soc. 76: 16-36.

Bewley, J. D. 1974. Protein synthesis and polyribosome stability upon desiccation of the aquatic moss *Hygrohypnum luridum*. Can. J. Bot. 52: 423-427.

Birse, E. M. 1957. Ecological studies on growth-form in bryophytes. II. Experimental studies on growth-form in mosses. J. Ecol. 45: 721-733.

Boudier, P. 1988. Différenciation structurale de l'épiderme du sporogone chez *Sphagnum fimbriatum* Wilson. [Structural differentiation of the epiderm of the sporogone of *Sphagnum fimbriatum* Wilson]. Ann. Sci. Nat. Bot. 13(8): 143-156.

Bowen, E. J. 1935. A note on the conduction of water in *Fimbriaria blumeana*. Ann. Bot. 49: 844-848.

Brandt, C. J. 1989. The size distribution of throughfall drops under vegetation canopies. Catena 16: 507-524.

Brockington, S., Glover, B., Duckett, J. G., and Pressel, S. 2013. The cuticle in *Marchantia*: An overlooked innovation in land plants. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.

Brodie, H. J. 1951. The splash-cup dispersal mechanism in plants. Can. J. Bot. 29: 224-230.

Buch, H. 1945. Über die Wasser- und Mineralstoffversorgung der Moose [Part 1]. Comment. Biol. Soc. Sci. Fenn. 9(16): 1-44.

Buch, H. 1947. Über die Wasser- und Mineralstoffversorgung der Moose [Part 2]. Comment. Biol. Soc. Sci. Fenn. 9(20): 1-61.

Budke, J. M., Goffinet, B., and Jones, C. S. 2011. A hundred-year-old question: Is the moss calyptra covered by a cuticle? A case study of *Funaria hygrometrica*. Ann. Bot. 107: 1279-1286.

Budke, J. M., Goffinet, B. and Jones, C. S. 2012. The cuticle on the gametophyte calyptra matures before the sporophyte cuticle in the moss *Funaria hygrometrica* (Funariaceae). Amer. J. Bot. 99: 14-22.

Budke, J. M., Goffinet, B., and Jones, C. S. 2013. Dehydration protection provided by a maternal cuticle improves offspring fitness in the moss *Funaria hygrometrica*. Ann. Bot. 111: 781-789.

Buryová, B. and Shaw, A. J. 2005. Phenotypic plasticity in *Philonotis fontana* (Bryopsida: Bartramiaceae). J. Bryol. 27: 13-22.

Callaghan, T. V., Collins, N. J., and Callaghan, C. H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. Oikos 31: 73-88.

Canny, M. J. 2001a. Contributions to the debate on water transport. Amer. J. Bot. 88: 43-46.

Canny, M. J. 2001b. Embolisms and refilling in the maize leaf lamina, and the role of the protoxylem lacuna. Amer. J. Bot. 88: 47-51.

Chater, C., Kamisugi, Y., Movahedi, M., Fleming, A., Cuming, A. C., Gray, J. E., and Beerling, D. J. 2011. Regulatory mechanism controlling stomatal behavior conserved across 400 million years of land plant evolution. Curr. Biol. 21: 1025-1029.

Clausen, E. 1952. Hepatics and humidity, a study of the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. Dansk Bot. Ark. 15: 5-80.

Clausen, E. 1964. The tolerance of hepatics to desiccation and temperature. Bryologist 67: 411-417.

Clayton-Greene, K. A., Collins, N. J, Green, T. G. A., and Proctor, M. C. F. 1985. Surface wax, structure and function in leaves of Polytrichaceae. J. Bryol. 13: 549-562.

Clee, D. A. 1943. The morphology and anatomy of *Fegatella conica* in relation to the mechanism of absorption and conduction of water. Ann. Bot. N. S. 7: 185-193.

Cook, M. E. and Graham, L. E. 1998. Structural similarities between surface layers of selected charophycean algae and bryophytes and the cuticles of vascular plants. Internat. J. Plant Sci. 159: 780-787.

Copeland, E. B. 1902. Mechanism of stomata. Ann. Bot. London 16: 327.

Crandall-Stotler, B. 2014. Bryophytes. Accessed 14 March 2015 at <http://bryophytes.plant.siu.edu/bryojustified.html>.

Daniels, A. E. D. 1998. Ecological adaptations of some bryophytes of the Western Ghats. J. Ecobiol. 10(4): 261-270.

Daniels, R. E. 1989. Adaptation and variation in bog mosses. Plants Today 2(4): 139-144.

Davey, M. C., Ellis-Evans, J. C. 1996. The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. J. Bryol. 19: 235-242.

Davy, V. A. de. 1927. L'action du Milieu sur les Mousses. Rev. Gen. de Bot. 39: 711-726.

Dhindsa, R. S. and Bewley, J. D. 1976. Plant desiccation: Polysome loss not due to ribonuclease. Science 191: 181-182.

Dilks, T. J. K. and Proctor, M. C. F. 1974. The pattern of recovery of bryophytes after desiccation. J. Bryol. 8: 97-115.

Dilks, T. J. K. and Proctor, M. C. F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol. 82: 97-114.

Duckett, J. G. and Ligrone, R. 1995. The formation of catenate foliar gemmae and the origin of oil bodies in the liverwort *Odontoschisma denudatum* (Mart.) Dum. (Jungermanniales): A light and electron microscope study. Ann. Bot. 76: 405-419.

Duckett, J. G. and Ligrone, R. 2003. What we couldn't have done if we'd stayed in Europe: Selection and serendipity in the Southern Hemisphere! Bull. Brit. Bryol. Soc. 80: 19-21.

Duckett, J. G. and Pressel, S. 2009. Extraordinary features of the reproductive biology of *Marchantia* at Thursley NNR. Field Bryol. 97: 2-11.

Duckett, J. G., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. S. 2009. Exploding a myth: The capsule dehiscence mechanism and the function of pseudostomata in *Sphagnum*. New Phytol. 183: 1053-1063.

Duckett, J., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. 2010a. The function and evolution of stomata in bryophytes. Field Bryol. 101: 38-40.

Duckett, J., Pressel, S., P'ng, K. M. Y., and Renzaglia, K. 2010b. The *Sphagnum* air-gun mechanism resurrected? Not with a closer look. New Phytol. 185: 889-891.

Duckett, J. G., Ligrone, R., Renzaglia, K. S., and Pressel, S. 2013. Pegged and smooth rhizoids in complex thalloid liverworts (Marchantiopsida): Structure, function and evolution. Bot. J. Linn. Soc. London (In press).

Dunlop J. W., Weinkamer R., and Fratzl, P. 2011. Artful interfaces within biological materials. Materials Today 14: 70-78.

Elumeeva, T. G., Soudzilovskaia, N. A., During, H. J., and Cornelissen, J. H. C. 2011. The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. J. Veg. Sci. 22: 152-164.

Fratzl, P., Kolednik, O., Fischer, F. D., and Dean M. N. 2016. The mechanics of tessellations – bioinspired strategies for fracture resistance. Chem. Soc. Rev. 45: 252-267.

Frenzke, L., Wanke, S., Isnard, S., Stoll, A., Neinhuis, C., Rowe, N. P. 2011. Stem biomechanics of the giant moss *Dendroligotrichum dendroides* s.l. and its significance for growth form diversity in mosses. J. Bryol. 33: 229-236.

Frey, W. and Kürschner, H. 1991. Morphologische und anatomische Anpassungen der Arten in terrestrisschen Bryophytengesellschaften entlang eines ökologischen Gradienten in der Judäischen Wüste. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 112: 529-552.

Garner, D. L B. and Paolillo, D. J. Jr. 1973. On the functioning of stomates in *Funaria*. Bryologist 76: 423-427.

Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat. J. Ecol. 4: 533-545.

Giordano, S., Castaldo Cobianchi, R., Basile, A., and Spagnuolo, V. 1989. The structure and role of hyaline parenchyma in the liverwort *Lunularia cruciata* (L.) Dum. Giornale Botanico Italiano 123: 169-176.

Glime, J. M. 1971. Response of two species of *Fontinalis* to isolation from stream water. Bryologist 74: 383-386.

Glime, J. M. 1987. Temperature optima of *Fontinalis novae-angliae*: Implications for its distribution. Symp. Biol. Hung. 35: 569-576.

Glime, J. M. and Carr, R. E. 1974. Temperature survival of *Fontinalis novae-angliae* Sull. Bryologist 77: 17-22.

Goebel, K. 1905. Organography of Plants. Part II. Special Organography. Translation by I. B. Balfour. Clarendon Press, Oxford.

Guerra, J., Martínez-Sánchez, J. J., Ros, R. M. 1992. On the degree of adaptation of the moss flora and vegetation in gypsiferous zones of the south-east Iberian Peninsula. J. Bryol. 17: 133-142.

Haig, D. 2013. Filial mistletoes: The functional morphology of moss sporophytes. Ann. Bot. 111: 337-345.

Hébant, C. 1973. Diversity of structure of the water-conducting elements in liverworts and mosses. J. Hattori Bot. Lab. 37: 229-234.

Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Lehre, Germany, 157 pp. + 80 Plates.

Hedenäs, L. 2001. Environmental factors potentially affecting character states in pleurocarpous mosses. Bryologist 104: 72-91.

Heegaard, E. 1997. Morphological variation within *Andreaea blyttii* in relation to the environment on Hardangervidda, western Norway: A quantitative analysis. Bryologist 100: 308-323.

Higuchi, M. and Imura, S. 1987. The effect of submersion on moss rhizoid characters. Hikobia 10: 59-63.

Jedrzejko, K. and Ziober, A. 1992. The bryophytes of chosen caves on the Krakow-Wielun upland and its relation to microclimate conditions and ecological differentiation of habitats. Ziemia Czestochowska 18: 107-151.

Johnson, A. and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. Bryologist 73: 682-686.

Jones V. A. S. and Dolan, L. 2012. The evolution of root hairs and rhizoids. Ann. Bot. 110: 205-212.

Kamerling, Z. 1897. Zur Biologie und Physiologie der Marchantiaceen. Flora 84: 1-68.

Kappen, L., Lange, O. L., Schulze, E. D., Evenari, M., and Buschbom, U. 1979. Ecophysiological investigations on lichens of the Negev desert. 6. Annual course of photosynthetic production of *Ramalina maciformis* (Del.) Bory. Flora Jena 168: 85-108.

Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. Arct. Alp. Res. 125: 308-315.

Klepper, B. 1963. Water relations of *Dicranum scoparium*. Bryologist 66: 41-54.

Kny, L. 1890. Bau und Entwicklung von *Marchantia polymorpha*. Parey, Berlin.

Koch, K., Frahm, J.-P., and Pollawatn, R. 2009. The cuticle of the *Buxbaumia viridis* sporophyte. Flora 204: 34-39.

Koster, K. L., Balsamo, R. A., Espinoza, C., and Oliver, M. J. 2010. Desiccation sensitivity and tolerance in the moss *Physcomitrella patens*: Assessing limits and damage. Plant Growth Reg. 62: 293-302.

Kürschner, H. K. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. Turk. J. Bot. 28: 73-84.

LaFarge-England, C. L. 1996. Growth form, branching pattern, and perichaetial position in mosses: Cladocarpy and pleurocarpy redefined. Bryologist 99: 170-186.

Lakatos, M. 2011. Lichens and bryophytes: Habitats and species. Ecol. Stud. 215: 65-87.

Lange, O. L. 1969. CO_2-Gaswechsel von Moosen nach Wasserdampfaufnahme aus dem Luftraum. Planta (Berlin) 89: 90-94.

Lepp, Heino. 2008. Thallose liverworts. Australian National Museum. Accessed 4 March 2015 at <https://www.anbg.gov.au/bryophyte/liverwort-thalose.html>.

Li, Y., Glime, J. M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. J. Bryol. 17: 59-70.

Ligrone, R., Duckett, J. G., and Renzaglia, K. S. 2000. Conducting tissues and phyletic relationships of bryophytes. Philosoph. Trans. Royal Soc. B 355: 795-814.

Lodge, E. 1959. Effects of certain cultivation treatments on the morphology of some British species of *Drepanocladus*. J. Linn. Soc. Bot. 56: 218-224.

Longton, R. E. 1972. Reproduction of Antarctic mosses in the genera *Polytrichum* and *Psilopilum* with particular reference to temperature. Brit. Antarct. Surv. Bull. 27: 51-96.

Longton, R. E. 1979. Studies on growth, reproduction and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. Bryologist 82: 325-367.

Longton, R. E. 1988. Adaptations and strategies of polar bryophytes. J. Linn. Soc. Bot. 98: 253-268.

Longton, R. E. and Greene, S. W. 1969. Relationship between sex distribution and sporophyte production in *Pleurozium schreberi* (Brid.) Mitt. Ann. Bot. 33: 107-126.

Mägdefrau, K. 1973. *Hydropogon fontinaloides* (Hook.) Brid., ein periodisch hydro-aerophytisches Laubmoos des Orinocos und Amazonas. Herzogia 3: 141-149.

Maier-Maercker, U. 1982. Accumulation of 86Rb and 43K ions in the cells surrounding the air pores of *Conocephalum conicum*. Zeits. Pflanzenphysiol. 105: 92-102.

Malta, N. 1921. Versuch uber die Wiederstandsfahigkeit der Moose gegen Austrocknung. Latv. Univ. Raksti 1: 125-129.

McConaha, M. 1939. Ventral surface specializations of *Conocephalum conicum*. Amer. J. Bot. 26: 353-355.

McConaha, M. 1941. Ventral structures effecting capillarity in the Marchantiales. Amer. J. Bot. 28: 301-306.

McLetchie, D. N. and Stark, L. R. 2006. Sporophyte and gametophyte generations differ in their thermotolerance response in the moss *Microbryum*. Ann. Bot. 97: 505-511.

Merced, A. 2015. Novel insights on the structure and composition of pseudostomata of *Sphagnum*. Amer. J. Bot. 102: 329-335.

Merced, A. and Renzaglia, K. S. 2013. Moss stomata in highly elaborated *Oedipodium* (Oedipodiaceae) and highly reduced *Ephemerum* (Pottiaceae) sporophytes are remarkably similar. Amer. J. Bot. 100: 2318-2327.

Morton, M. R. 1977. Ecological studies of grassland bryophytes. Ph. D. Thesis, University of London.

Mulder, C. P. H., Uliassi, D. D., Doak, D. F. 2001. Physical stress and diversity-productivity relationships: The role of positive interactions. Proc. Natl. Acad. Sci. USA 98: 6704-6708.

Nakatsubo, T. 1994. The effect of growth form on the evaporation in some subalpine mosses. Ecol. Res. 9: 245-250.

Niklas, K. J. 1992. Plant Biomechanics: An Engineering Approach to Plant Form and Function, University Chicago Press, Chicago, USA, 607 pp.

Nörr, M. 1974. Trockenrisistenz bei Moosen. Flora Jena 163: 371-378.

Odu, E. A. 1978. The adaptive importance of moss rhizoids for attachment to the substratum. J. Bryol. 10: 163-181.

Oliver, M. J. and Bewley, J. D. 1984. Desiccation and ultrastructure in bryophytes. Advances in Bryology 2: 91-131.

Oliver, M. J., Wood, A. J., and O'Mahony, P. 1998. "To dryness and beyond" – preparation for the dried state and rehydration in vegetative desiccation-tolerant plants. Plant Growth Reg. 24: 193-201.

Oliver, M. J., Velten, J., and Mishler, B. D. 2005. Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats. Integr. Compar. Biol. 45: 788-799.

Patidar, K. C. 1988. Morphological variation of two isolated geographical field populations of *Asterella angusta* (Steph.) Kachroo. Yushania 5(1): 7-18.

Paton, J. A. and Pearce, J. V. 1957. The occurrence, structure and functions of the stomata in British bryophytes. Trans. Brit. Bryol. Soc. 3: 228-259.

Penman, H. L. 1948. Natural evaporation from open water, bare soil and grass. Proc. Roy. Soc. London A194: 120-145.

Pressel, S. 2006. Effects of de- and rehydration on food-conducting cells in the moss *Polytrichum formosum*: A cytological study. Ann. Bot. 98: 67-76.

Pressel, S. 2007. Experimental Studies of Bryophyte Cell Biology, Conservation, Physiology and Systematics. Ph.D. Dissertation. University of London, London.

Pressel, S. and Duckett, J. G. 2010. Cytological insights into the desiccation biology of a model system: Moss protonemata. New Phytol. 185: 944-963.

Pressel, S. and Duckett, J. 2011. Bryophyte surfaces; New functional perspectives from Cryo-Scanning Electron Microscopy. Field Bryol. 104: 50-53.

Pressel, S., Davis, E. C., Ligrone, R., and Duckett, J. G. 2008a. An ascomycetous endophyte induces branching and septation of the rhizoids in the leafy liverwort family the

Schistochilaceae (Jungermanniidae, Hepaticopsida). Amer. J. Bot. 95: 531-541.

Pressel, S., Ligrone, R., and Duckett, J. G. 2008b. Cellular differentiation in moss protonemata: A morphological and experimental study. Ann. Bot. 102: 227-245.

Pressel, S., Ligrone, R., and Duckett, J. G. 2008c. Chapter Six: The ascomycete *Rhizoscyphus ericae* elicits a range of host responses in the rhizoids of leafy liverworts: An experimental and cytological analysis. Field. Bot. 47: 59-72.

Pressel, S., Bidartondo, M. I., Ligrone, R., and Duckett, J. G. 2010. Fungal symbioses in bryophytes: New insights in the twenty-first century. Phytotaxa 9: 238-253.

Pressel, S., Duckett, J. G., and Bidartondo, M. I. 2012. Liverwort fungal interactions; the dawn of mycotrophism. Field Bryol. 107: 38-39.

Proctor, M. C. F. 1979. Structure and eco-physiological adaptations in bryophytes. In: Clarke, G. C. S. and Duckett, J. G. (eds.). Bryophyte Systematics, Systematic Association special volume 14, Academic Press, London, pp. 479-509.

Proctor, M. C. F. 1980. Diffusion resistances in bryophytes. In: Ford, E. D., and Grace, J. (eds.). Plants and their Atmospheric Environment. Symp. Brit. Ecol. Soc., pp. 219-229.

Proctor, M. C. F. 1981. Diffusion resistances in bryophytes. In: Grace, J., Ford, E. D., and Jarvis, P. G. (eds.). Plants and Their Atmospheric Environment. Blackwell, Oxford, UK, pp. 219-229.

Proctor, M. C. F. 1982. Physiological ecology, water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman & Hall, London, pp. 333-382.

Proctor, M. C. F. 2000. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Proctor, M. C. F. 2010. Trait correlations in bryophytes: Exploring an alternative world. New Phytol. 185: 1-3.

Proctor, M. C. F. and Pence, V. C. 2002. Vegetative tissues: Bryophytes, vascular resurrection plants and vegetative propagules. In: Pritchard, H. and Black, M. (eds.). Desiccation and Plant Survival. CABI Publishing, Wallingford, UK, pp. 207-237.

Proctor, M. C. F. and Tuba, Z. 2002. Poikilohydry and homoihydry: Antithesis or spectrum of possibilities? New Phytol. 156: 327-349.

Proctor, M. C. F., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., and Mishler, B. D. 2007. Desiccation-tolerance in bryophytes: A review. Bryologist 110: 595-621.

Raven, J. A. 1993. The evolution of vascular plants in relation to quantitative functioning of dead water-conducting cells and stomata. Biol. Rev. 68: 337-363.

Raven, J. A. 2002. Selection pressures on stomatal evolution. New Phytol.153: 371-386.

Raven, J. A. and Handley, L. L. 1987. Transport processes and water relations. New Phytol. 106: 217-233.

Raven, P. H., Evert, R. F., and Eichhorn, S. E. 2005. Biology of Plants. W. H. Freeman Co., N. Y., p. 348.

Read, D. J., Duckett, J. G., Francis, R., Ligrone, R., and Russell, A. 2000. Symbiotic fungal associations in 'lower' land plants. Philosoph. Trans. Royal Soc. B 355: 815-832.

Riccia cavernosa Hoffm. 2012. Botanical Society of the British Isles. Accessed 14 March 2015 at <http://www.s231645534.websitehome.co.uk/Riccia%20cavernosa.htm>.

Rice, S. K. 2012. The cost of capillary integration for bryophyte canopy water and carbon dynamics. Lindbergia 35: 53-62.

Rice S. K. and Schneider, N. 2004. Cushion size, surface roughness, and the control of water balance and carbon flux in the cushion moss *Leucobryum glaucum* (Leucobryaceae). Amer. J. Bot. 91: 1164-1172.

Rice, S. K., Collins, D., and Anderson, A. M. 2001. Functional significance of variation in bryophyte canopy structure. Amer. J. Bot. 88: 1568-1576.

Richardson, D. H. S. 1981. The Biology of Mosses. John Wiley & Sons, Inc., N. Y., 220 pp.

Rixen, C. and Mulder, C. P. H. 2005. Improved water retention links high species richness with increased productivity in Arctic tundra moss communities. Oecologia 146: 287-299.

Romose, V. 1940. Ökologische Untersuchungen uber *Homalothecium sericeum*, seine Wachstumsperioden und seine Stoffproduktion. Dansk Bot. Ark. 10: 1-134.

Rossi, S. E., Callaghan, T. V., Sonesson, M., and Sheffieldi, E. 2001. Variation and control of growth-form in the moss *Hylocomium splendens*. J. Bryol. 23: 283-292.

Rowntree, J. K., Duckett, J. G., Mortimer, C. L., Ramsay, M., and Pressel, S. 2007. Formation of specialized propagules resistant to desiccation and cryopreservation in the threatened moss *Ditrichum plumbicola* Crundw. (Ditrichales, Bryopsida). Ann. Bot. 100: 483-496.

Rundel, P. W. and Lange, O. L. 1980. Water relations and photosynthetic response of a desert moss. Flora 169: 329-335.

Sand-Jensen, K. and Hammer, K. J. 2012. Moss cushions facilitate water and nutrient supply for plant species on bare limestone pavements. Oecologia 170: 305-312.

Sarafis, V. 1971. A biological account of *Polytrichum commune*. N. Zeal. J. Bot. 9: 711-724.

Schofield, W. B. 1981. Ecological significance of morphological characters in the moss gametophyte. Bryologist 84: 149-165.

Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. Planta 124: 51-60.

Schröder, G. 1886. Über die Austrocknungsfähigkeit der Pflanzen. Untersuchungen aus dem Botanischen Institut zu Tübingen, II: 1-53.

Seki, T. and Yamaguchi, T. 1985. The effect of climatic factors on the floristic diversity of bryophytes in the Yaeyama Islands, the Ryuku Archipelago, southern Japan. In: Hara, H. (ed.). Origin and evolution of diversity in plants and plant communities, Academic Scientific Book Co. Inc., Tokyo, pp. 60-76.

Shaw, A. J. and Goffinet, B. 2000. Bryophyte Biology. Cambridge University Press, Cambridge.

Skre, O., Oechel, W. C., and Miller, P. M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can. J. Forest. Res. 13: 860-868.

Smith, M., Bruhn, J., and Anderson, J. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. Nature 356: 428-431

Smith, R. I. L. 1988. Aspects of cryptogam water relations at a continental Antarctic site. Polarforschung 58: 139-153.

Stark, L. R. 2002. New frontiers in bryology: Phenology and its repercussions on the reproductive ecology of mosses. Bryologist 105: 204-218.

Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year

period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.

Stark, L. R., Mishler, B. D., and McLetchie, D. N. 2000. The cost of realized sexual reproduction: assessing patterns of reproductive allocation and sporophyte abortion in a desert moss. Amer. J. Bot. 87: 1599-1608.

Stark, L. R., Oliver, M. J., Mishler, B. D., and McLetchie, D. N. 2007. Generational differences in response to desiccation stress in the desert moss *Tortula inermis*. Ann. Bot. 99: 53-60.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2013. The desert moss *Pterygoneurum lamellatum* exhibits inducible desiccation tolerance: Effects of rate of drying on shoot damage and regeneration. Amer. J. Bot. 100: 1522-1531.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2014. Physiological history may mask the inherent inducible desiccation tolerance strategy of the desert moss *Crossidium crassinerve*. Plant Biol. 16: 935-946.

Steere, W. C. 1976. Ecology, phytogeography and floristics of Arctic Alaskan bryophytes. J. Hattori Bot. Lab. 41: 47-72.

Trachtenberg, S. and Zamski, E. 1979. The apoplastic conduction of water in *Polytrichum juniperinum* Willd. gametophytes. New Phytol. 83: 49-52.

Tuba, Z. 1984. Changes in the photosynthetic pigment system of the drought tolerant *Tortula ruralis* during a daily desiccation. Proc. Third Meeting Bryologists from Centr. and East Eur. Univ. Karlova, Praha, pp. 343-352.

Tuba, Z. 1985. Photosynthetic pigment responses in *Tortula ruralis* during daily desiccation. Abstr. Bot. 9, Suppl. 2: 231-239.

Vincent, J. 2012. Structural Biomaterials. Princeton University Press, USA, 240 pp.

Vishvakarma, K. S. and Kaul, A. 1988. Influence of moisture levels on growth of *Plagiochasma appendiculatum* Lehm. et Lindb. and *Reboulia hemisphaerica* (L.) Raddi on a comparative basis. Cryptog. Bryol. Lichénol. 9: 337-341.

Vitt, D. H., Crandall-Stotler, B., and Wood, A. J. 2014. Bryophytes, survival in a dry world through tolerance and avoidance. In: Rajakaruna, N., Boyd, R. S., and Harris, T. B. (eds.). Plant Ecology and Evolution in Harsh Environments. Nova Science Publishers, Inc., New York, NY, pp. 267-295.

Volk, O. H. 1984. Beiträge zur Kenntnis der Marchantiales in Suedwest-Afrika/Namibia. IV. Zur Biologie einiger Hepaticae mit besonderer Beruecksichtigung der Gattung *Riccia*. [Contribution to the knowledge of the Marchantiales in Southwest Africa/Namibia. IV. The biology of some Hepaticae with particular consideration of the genus *Riccia*.]. Nova Hedw. 39: 117-144.

Watson, E. V. 1971. Structure and Life of Bryophytes. 3rd edn. Hutchinson & Co. Ltd., London.

Wood, A. J. 2007. The nature and distribution of vegetative desiccation tolerance in hornworts, liverworts and mosses. Bryologist 110: 163-177.

Yakubu, M. L., Yusop, Z., and Fulazzaky, M. A. 2016. The influence of rain intensity on raindrop diameter and the kinetics of tropical rainfall: Case study of Skudai, Malaysia. Hydrol. Sci. J. 61: 944-951.

Zajączkowska, U., Grabowska, K., Kokot, G., and Kruk, M. 2016. On the benefits of living in clumps. A case study on *Polytrichastrum formosum.* Plant Biol. (in review).

Zehr, D. R. 1979. Phenology of selected bryophytes in southern Illinois. Bryologist 82: 29-36.

Zheng, Y., Xu, M., Zhao, J., Zhang, B., Bei, S., and Hao, L. 2010. Morphological adaptations to drought and reproductive strategy of the moss *Syntrichia caninervis* in the Gurbantunggut Desert, China. Arid Land Research and Management 25: 116-127.

Ziegler, H. 1987. The evolution of stomata. In: Zeiger, E., Farquhar, G. D., Cowan, I. R. Stomatal Function. Stanford University Press, Stanford, CA, pp. 29-57.

Zotz, G., Schweikert, A., Jetz, W., and Westerman, H. 2000. Water relations and carbon gain in relation to cushion size in the moss *Grimmia pulvinata* (Hedw.) Sm. New Phytol. 148: 59-67.

CHAPTER 7-4a

WATER RELATIONS: LEAF STRATEGIES – STRUCTURAL

TABLE OF CONTENTS

Overlapping Leaves 7-4a-4
Thickened Leaf 7-4a-5
Concave Leaves 7-4a-7
Cucullate Leaves 7-4a-10
Plications 7-4a-10
Revolute and Involute Margins 7-4a-11
Borders 7-4a-12
Leaf Teeth 7-4a-14
Teniolae 7-4a-15
Costa 7-4a-15
Stereids 7-4a-16
Lamellae 7-4a-17
Lobules and Storage Organs 7-4a-22
Hair Points 7-4a-23
Nucleation 7-4a-25
Papillae 7-4a-25
Leaf Bases and Alar Cells 7-4a-30
Leaf Cell Shape 7-4a-31
Porose Cells 7-4a-31
Hyalocysts 7-4a-31
Cancellinae 7-4a-34
Cell Structure 7-4a-35
    Cell Walls 7-4a-35
    Oil Bodies 7-4a-38
    Vacuoles 7-4a-40
    Slime Papillae 7-4a-41
Summary 7-4a-42
Acknowledgments 7-4a-42
Literature Cited 7-4a-42

CHAPTER 7-4a

WATER RELATIONS: LEAF STRATEGIES – STRUCTURAL

Figure 1. ***Campylopus introflexus*** demonstrating the ability of water to cling and collect on the thin, wiry leaves. Photo by Michael Lüth, with permission.

Much of what we know about water uptake by bryophytes has been through observation. While the observations are probably valid, broad generalizations have emerged and these have been applied to all mosses, especially by non-bryologists, and can lead to inappropriate experiments and conclusions.

Larson (1981) experimented with three species of bryophytes (and 8 lichens) using a "raining" wind tunnel environment to determine the effects of various structures on water uptake and storage. Larson found that the time required to reach saturation did not differ between lichens and mosses, varying from three minutes in the moss ***Polytrichum juniperinum*** (Figure 2) to over 300 minutes in the lichen ***Stereocaulon saxatile***. The rate of absorption increases with the ratio of surface area to weight, making it extremely rapid in finely divided plants. Hence, comparison of leaf structure and plant form become important in considering the role of bryophytes in the water cycling of an ecosystem (Proctor *et al*. 1998; Wu *et al*. 2007).

Schofield (1981) considered leaf shape, arrangement, orientation, surface ornamentation, and detailed anatomy to be important in influencing water movement. These adaptations are complemented by branch arrangement, stem cortical cells, rhizoid structure, and presence of paraphyllia.

Figure 2. ***Polytrichum juniperinum*** hydrated (**left**) and dry (**right**) showing change in leaf position to wrap around stem. Photo by Michael Lüth, with permission.

Bryophytes hold their water in three ways (Proctor *et al*. 1998): **apoplastic** water in cell-wall capillary spaces and held by matric forces; **symplastic** (internal osmotic) water; external capillary water. For many bryophytes, the external capillary water is a highly important, albeit variable, component. This external water complicates any measurements of relative water content (RWC) because it makes measurement of the bryophyte at full turgor a difficult endeavor. Proctor *et al*. found that full-turgor water ranged from 110% dry weight (dw) in ***Syntrichia ruralis*** (Figure 3) and ***Andreaea alpina*** (Figure 4) to 1400% dw or more in ***Dumortiera hirsuta*** (Figure 5) and ***Conocephalum conicum*** (Figure 6-Figure 7). Most species had an osmotic potential ($\Psi\pi$) at full turgor of -1.0 to -2.0 MPa, but thallose liverworts had values that were much less negative (-0.35 to -0.64 MPa).

Figure 3. ***Syntrichia ruralis*** with raindrops, a moss with low water content. Photo by Peggy Edwards, with permission.

Figure 4. ***Andreaea alpina***, a moss with low water content. Photo by Andrew Hodgson, with permission.

Figure 5. ***Dumortiera hirsuta***, a thallose liverwort that holds a high water content. Photo by Li Zhang, with permission.

Figure 6. ***Conocephalum conicum***, a thallose liverwort that holds a high water content. Photo by Robert Klips, with permission.

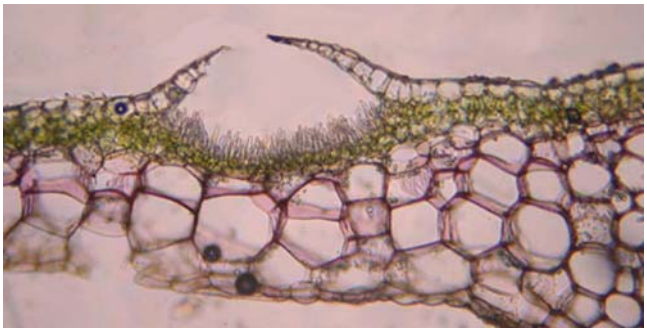

Figure 7. ***Conocephalum conicum*** thallus section with pore From website of the Botany Department, University of British Columbia, with permission.

Pressel *et al*. (2009) pointed out that despite the ancient history of liverworts, we know little about the physiology of their desiccation tolerance. Desiccation causes a number of cytological changes in liverworts, including fragmentation of the vacuole, rounding of the chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged, all responses that are similar to those of mosses and **tracheophytes** (non-bryophyte plants; plants with lignified vascular tissue). Furthermore, chlorophyll fluorescence shows half–recovery within minutes to 2 hours, but requires 24-48 hours to reach normal, unstressed values. And like desiccation tolerance in mosses, the de- and repolymerization of the cortical microtubule cytoskeleton

are associated with de- and rehydration. But liverworts have oil bodies, and these play a role unknown in mosses, as will be seen below.

Guerra *et al*. (1992) described the adaptations of xeric mosses in the gypsiferous zones of the southeast Iberian Peninsula, listing 15 modifications for conserving water. I have included these and some of my own observations here.

Overlapping Leaves

Most bryophytes have their leaves inserted at angles on the stem. In some cases, especially leafy liverworts (Figure 8), these are **incubous** in arrangement [leaves overlapping from base to tip like shingles on a roof, with the part of the leaf closer to the stem base being nearer the substrate (ventral) and the more apical side emerging on the upper (dorsal) side of the stem], whereas others are **succubous** [basal edge dorsal, apical edge ventral – the leaf succumbs to the leaf above it].

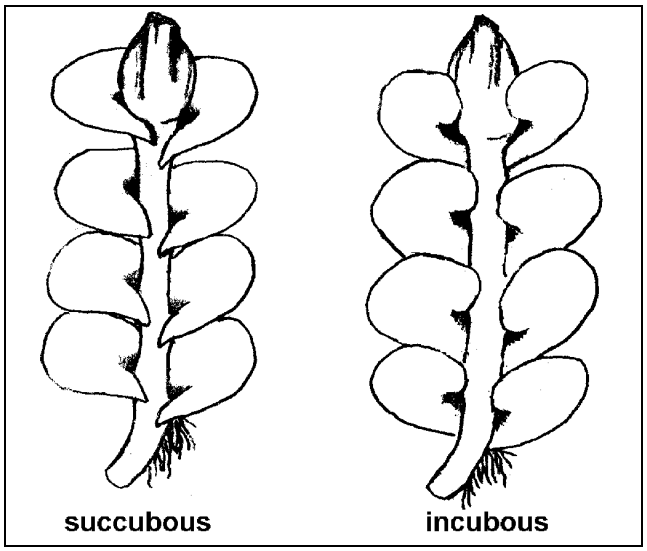

Figure 8. Succubous leaf arrangement of liverworts such as ***Jungermannia*** (**left**) and incubous arrangement of those such as ***Calypogeja*** (**right**). Note the decurrent leaf bases in the liverwort on the left. Redrawn by Margaret Minahan from Iwatsuki.

Clee (1937) found that in the succubous ***Plagiochila asplenioides*** var. ***major*** (Figure 9), water could move up to 3.7 cm in one minute. However, with the incubous arrangement, water moved less than 1 cm per minute. On the other hand, Basile and Basile (1987) questioned the role of the incubous vs. succubous leaf orientation in water conduction. They found that conduction proceeds equally in both orientations and that there is no correlation between the direction of leaf overlap and the angle of the substrate slope where they commonly grow. This seems reasonable since water coming from the top in rainfall would be presented with the opposite direction from water coming from beneath the branch. Hence, we could consider the branches in Figure 8 to be the above and below presentations of the same plant. Certainly if water is available from both above and below, it should make little difference if the plant is succubous or incubous. We need experiments to compare the effect on liverworts that form protruding shelves, those that are growing upright from a substrate, those that are adnate to a vertical surface, and those that grow horizontally adnate to a substrate. Then we need to compare the direction of the water source – base or tip of plant, dorsal or ventral surface.

Figure 9. ***Plagiochila asplenioides*** with overlapping, succubous leaves. Photo by Michael Lüth, with permission.

Among mosses, Bowen (1933) considered the erect habit of leaves to hold and conduct more water than spreading leaves. This effect is enhanced if the leaves have **decurrent** bases (extensions of the leaf base down the stem; Figure 8).

Bayfield (1973) found that as water content declined in ***Polytrichum commune*** (Figure 10), the leaf arrangement changed (see also changes in ***Polytrichum juniperinum*** Figure 2). As the moisture decreased, the leaves wrapped closer around the stem, seemingly increasing moisture retention, a phenomenon that makes ***Hedwigia ciliata*** (Figure 11) almost unrecognizable when wet if one is only familiar with the dry state. Bayfield also found that external conduction is possible in the capillary spaces between the stem and the overlapping leaf bases. In the endohydric ***Polytrichum*** species, the loss of water is controlled by a complex series of changes in the leaf arrangement, whereas in the ectohydric ***Racomitrium lanuginosum*** (Figure 12-Figure 13), little or no mechanical control is exercised over water loss. It is likely that all ***Polytrichum*** (Figure 2, Figure 10) species benefit from this movement of the leaves upon drying.

Figure 10. ***Polytrichum commune*** showing the dry lower leaves that are beginning to wrap around the stem compared to the wide-spreading upper leaves that are well hydrated. Photo by Michael Lüth, with permission.

Figure 11. ***Hedwigia ciliata*** showing wet leaves (**upper left**) and dry leaves (**diagonally across lower right**) as a result of drying from the edge of the mat inward. The plants were growing on exposed boulders at the base of a cliff. Photo by Janice Glime.

Figure 12. ***Racomitrium lanuginosum*** dry showing twisted leaves and prominence of awns at the leaf tips, but little mechanical control over water loss. Photo by Michael Lüth, with permission.

Figure 13. ***Racomitrium lanuginosum*** wet showing transparent awns that are much less conspicuous than in dry plants. Photo by Des Callaghan, with permission.

Leaves Curving or Twisting upon Drying

Many species have leaves that curve or twist when they dry, particularly those in xeric habitats. These leaves curve toward the stem and thus reduce the exposed surface area. Among these are ***Campylostelium pitardii*** (Figure 14), ***Phascum cuynetii***, and ***Pterygoneurum sampaianum***.

Figure 14. ***Campylostelium pitardii*** with capsules, a species whose leaves curve or twist when dry. Photo by Proyecto Musgos, through Creative Commons.

Thickened Leaf

Many leaves partially protect themselves from water loss by having all or part of the leaf more than one cell thick. This is a common character for the borders and costa, where it most likely serves for support and possibly water movement, but in the leaf **lamina**, this reduces the exposed surface area (Figure 17).

Some leaves are **bistratose** in the upper part of the leaf, *i.e.* the part most exposed when the plant is dry. Among these are the xerophytic species ***Syntrichia caninervis*** (Figure 115) subsp. ***spuria***, ***Dicranella varia*** (Figure 15), and ***Didymodon australasiae*** (Figure 16) (Guerra *et al*. 1992).

Figure 15. ***Dicranella varia***. Note the twisted leaves on the dry mosses in the foreground. Photo by J. C. Schou, with permission.

Figure 16. ***Didymodon australasiae*** showing leaves curved around the stem in this dry state. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species protect the photosynthetic cells with hyaline cells, as in ***Leucobryum*** (Figure 18) and ***Octoblepharum*** (Figure 19). ***Fissidens grandifrons*** (Figure 20) differs from most other members of the genus ***Fissidens*** by having leaves that are multiple cell layers thick, most likely an adaptation to its habitat in fast-flowing water of streams and waterfalls. ***Fissidens*** accomplishes a degree of protection and provides capillary water-holding spaces by creating a pocket (Figure 21-Figure 24), giving this region a thickness of two layers of cells; the next leaf toward the apex often fits into this pocket. But this flattened moss nevertheless moves water slowly through its external surface (Table 1).

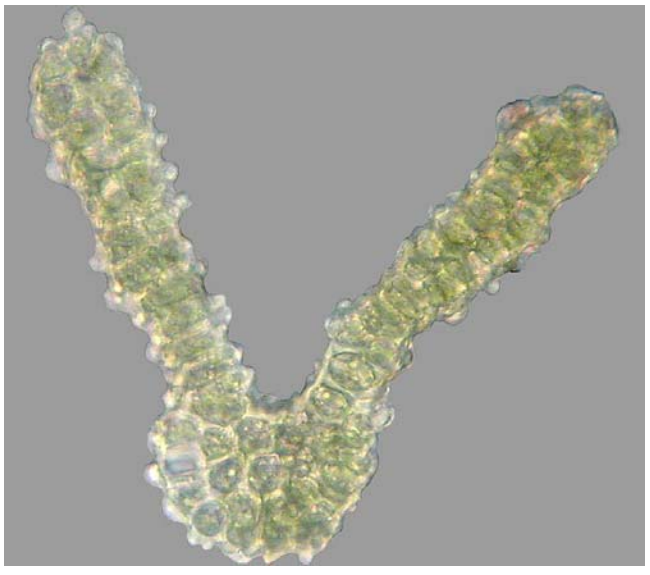

Figure 17. ***Grimmia anomala*** leaf section showing double layer of cells in parts of the lamina and papillae on the cells. Photo by Michael Lüth, with permission.

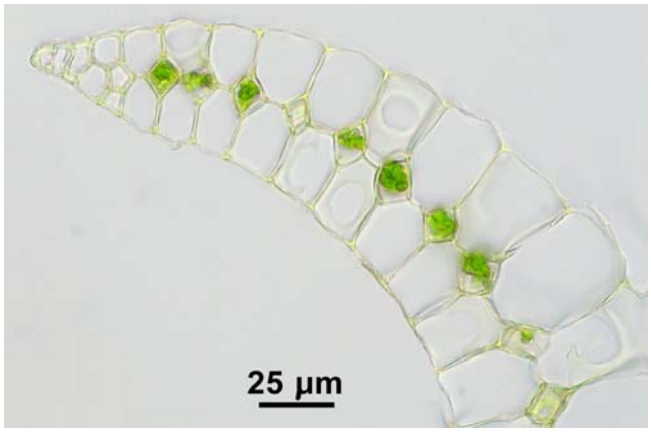

Figure 18. ***Leucobryum glaucum*** leaf cross section showing multiple layers with outer hyaline cells and central photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

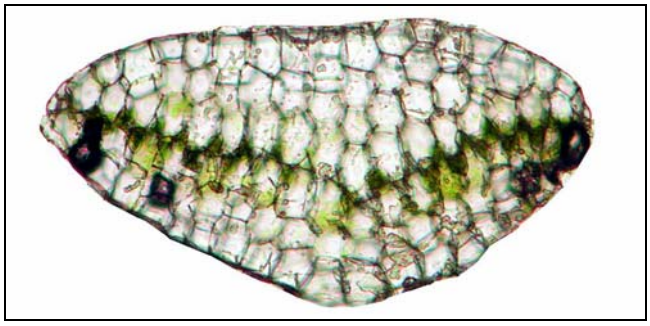

Figure 19. ***Octoblepharum albidum*** leaf cross section showing multiple layers of hyaline cells. Photo by Michael Lüth, with permission.

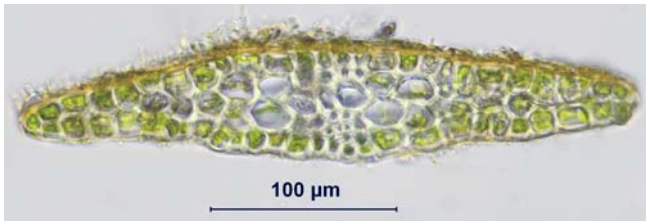

Figure 20. ***Fissidens grandifrons*** leaf cross section showing multiple layers that help this species to survive in torrents of water in waterfalls and snowmelt streams. These layers may also aid its survival when the water recedes, stranding it out of the water. Photo by Li Zhang, with permission.

Figure 21. ***Fissidens asplenioides*** showing flattened branch with each leaf fitting into the pocket of the one below it. Photo by Michael Lüth, with permission.

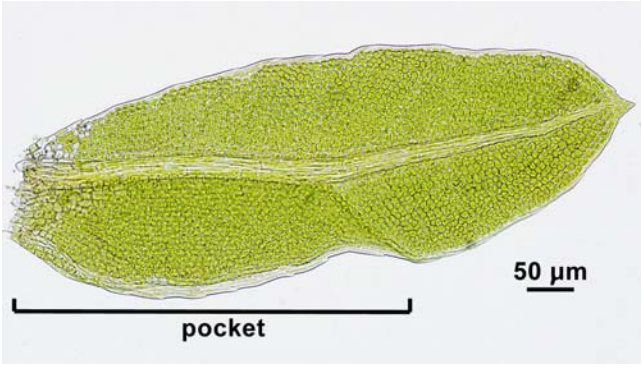

Figure 22. ***Fissidens crispus*** leaf showing pocket. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 23. ***Fissidens taxifolius*** leaves showing one leaf fitting into pocket of the next. Photo by Walter Obermayer, with permission.

Figure 24. ***Fissidens taxifolius*** leaf cross section through pocket. Note that the costa forms the region where the two halves join. Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Concave Leaves

Proctor (1979a) found that many taxa of ectohydric mosses have concave leaves (*e.g.* Figure 25-Figure 26). When examined in moist weather, the concavities on the upper sides of the leaves will generally be full of water. This helps to solve the problem of gas exchange by exposing one surface to the atmosphere while keeping the other surface bathed in water. And most of the CO_2 needed for photosynthesis comes from respiration in the soil and litter. Gas diffusion in air is about 10^4 times faster than in water (Proctor 1982). Other mosses, like ***Campylopus*** (Figure 1) and ***Polytrichum*** (Figure 2, Figure 10), are able to roll their leaves, like some grasses, when they are dry. In this mode, mosses like ***Syntrichia ruralis*** (Figure 28) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).

Figure 25. The moss ***Scleropodium touretii*** illustrating deeply concave leaves. Photo by Michael Lüth.

Figure 26. ***Pseudoscleropodium purum*** showing concave leaves. Photo by Aimon Niklasson, with permission.

Figure 27. ***Syntrichia ruralis*** dry. Photo by Janice Glime.

Figure 28. ***Syntrichia ruralis*** wet. Photo by Janice Glime.

Leaf spreading upon re-moistening is rapid in most bryophytes. Yenhung Li (unpublished data) found that in ***Sphagnum*** sp., ***Ptilium crista-castrensis*** (Figure 29), ***Pleurozium schreberi*** (Figure 30), and ***Dicranum polysetum*** (Figure 32), the first leaves spread within 1.5 to 2 seconds of receiving water (Table 1). To wet all the leaves in pieces 0.7 cm long required less than 2 minutes for most taxa, but required 24 minutes in ***Rhodobryum ontariense*** (Figure 31). The highest rate of conduction among the 15 taxa was in ***Pleurozium schreberi*** (140 mm min^{-1}).

Figure 29. ***Ptilium crista-castrensis***, a moss that rewets quickly. Photo by Michael Lüth, with permission.

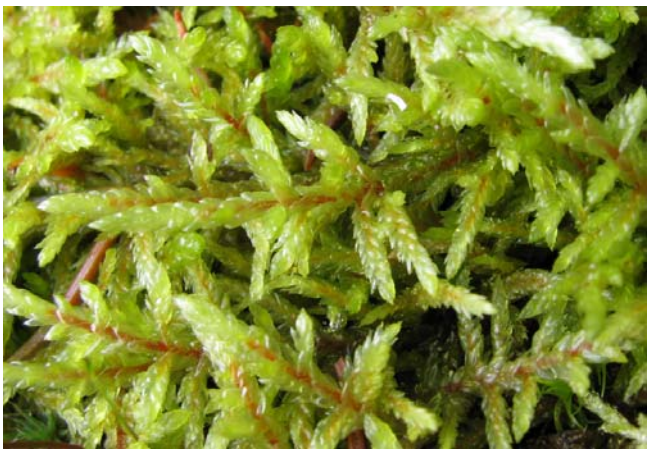

Figure 30. ***Pleurozium schreberi***, a feather moss that rewets quickly. Photo by Janice Glime.

Figure 31. ***Rhodobryum ontariense***, a moss that rewets very slowly. The dense cluster of leaves are all at the top of the stem. Photo by Janice Glime.

Figure 32. ***Dicranum polysetum***, a boreal forest moss that rewets quickly. Photo by O. V. Ivanov, with permission.

Table 1. Mean time required for leaf spreading and conduction rate after rewetting along 0.7 cm branches in 15 species of bryophytes (n = 30 & 10 respectively). Based on Yenhung Li, unpublished data.

Species	sec for spreading	conduction mm/min
Ptilium crista-castrensis	2	0.93
Dicranum polysetum	2	70.00
Pleurozium schreberi	5	140.00
Hedwigia ciliata	5	11.48
Climacium dendroides	8	21.00
Fontinalis duriaei	9	2.60
Dicranella heteromalla	10	11.48
Lophozia barbata	10	24.1
Anomodon attenuatus	14	0.06
Fontinalis antipyretica var. *gigantea*	26	27.5
Porella platyphylla	34	0.75
Sphagnum sp.	90	6.0
Bryum pseudotriquetrum	149	0.82
Fissidens adianthoides	284	0.08
Rhodobryum ontariense	1421	0.06

Li found some indication that small leaves can spread more quickly than large ones, at least in ***Fontinalis***. ***Fontinalis duriaei*** (Figure 33) has smaller and thinner leaves than does ***F. antipyretica*** var. ***gigantea*** (Figure 34-Figure 35), and ***F. duriaei*** can spread its leaves in 1/3 the time required for ***F. antipyretica*** var. ***gigantea***. However, the difference may be due to the stiffness of the **keel** (leaf fold; Figure 35) in ***F. antipyretica*** var. ***gigantea***, whereas ***F. duriaei*** has flat leaves.

Figure 33. ***Fontinalis duriaei***, a species with flat, relatively narrow leaves that spread more quickly than larger leaves with a keel in ***Fontinalis antipyretica*** var. **gigantea**. Photo by Janice Glime.

Among the slowest species to re-wet in Li's study were ***Fissidens adianthoides*** (Figure 36) and ***Rhodobryum ontariense*** (Figure 31), both for rate of conduction and leaf wetting. ***Fissidens adianthoides*** has leaves that are large and partly two-layered. There is little overlap between the leaves in this genus except at the two-layered pocket (Figure 37), and Church and Nelson (unpubl data) noted that when the leaves of ***F. adianthoides*** are dry there is little or no overlap even at the pocket. Therefore, lack of capillary space may account for its slow response. The slowness of ***Rhodobryum ontariense***, which has all its leaves crowded at the top of the stem like a palm tree (Figure 31), may likewise be explained by lack of capillary spaces (Figure 38). Below the crowded rosette of leaves at the apex are very reduced scale-like leaves along the stem, providing little capillary space and rendering it the slowest among the 15 species observed by Li. It required 123 minutes for the water to travel 0.7 cm up the stem! Although Li's data indicate a slight trend for rapid conduction to be coupled with rapid leaf spreading, there are enough exceptions to indicate that the relationship is not so simple.

Figure 34. ***Fontinalis antipyretica*** showing keeled leaves that spread slowly but that conduct water externally relatively rapidly. Photo by Jan-Peter Frahm, with permission.

Figure 35. ***Fontinalis antipyretica*** leaf showing keel (**lower side of image**). Photo by Malcolm Storey, through Creative Commons.

Figure 36. ***Fissidens adianthoides***, a moss providing little capillary space, hence slow external conduction. Photo by Niels Klazenga, with permission.

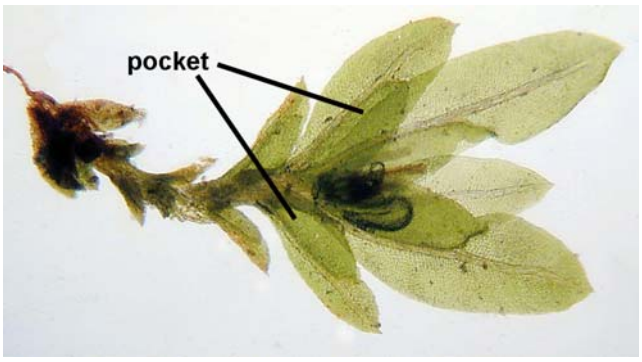

Figure 37. ***Fissidens arnoldii*** showing the overlap created by leaf pockets where the leaf blade has two, but separated, layers. Photo by Michael Lüth, with permission.

Figure 38. ***Rhodobryum ontariense*** dry, with its leaves twisted upward. Note the bare stem that seemingly provides no capillary spaces for external conduction. Photo by Michael Lüth, with permission.

Cucullate Leaves

Cucullate is hooded or boat-shaped, referring to the apex of leaves in this case. The cavity created by this leaf form is able to hold water, in part due to surface tension. An example of this is the moss ***Phascum cuynetii***; some ***Sphagnum*** (Figure 39) species also have cucullate leaves.

Figure 39. ***Sphagnum*** sp. from the Neotropics showing cucullate leaves. Photo by Michael Lüth, with permission.

Plications

Plications, or Japanese fanfolds, in the leaf may reduce evaporation by reducing the exposed area and creating nearly dead space between the folds. On the other hand, it might simply be a means of neatly folding the leaf as it dries and loses the turgidity that kept it concave. These plications are present in ***Brachythecium*** (Figure 40), ***Coscinodon*** (Figure 41-Figure 43), and ***Hamatocaulis vernicosus*** (=*Drepanocladus vernicosus*; Figure 44), among others. Some taxa exhibit these only as they are drying or dry, so the system is responsive to water loss. When it is rehydrated, the plications permit the leaf to expand.

Figure 40. ***Brachythecium*** leaves showing plications. Photo by Bob Klips, with permission.

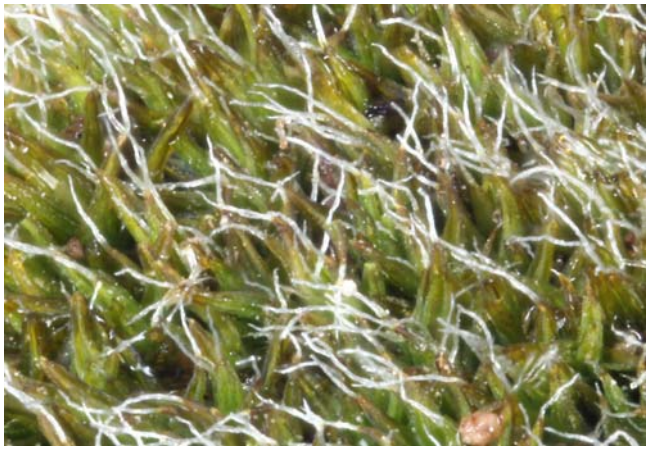

Figure 41. ***Coscinodon cribrosus***. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

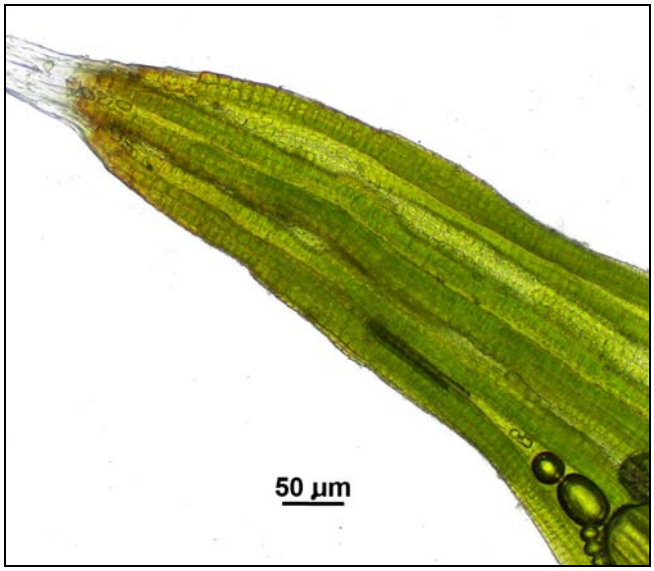

Figure 42. ***Coscinodon cribrosus*** leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 43. ***Coscinodon cribrosus*** leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 44. ***Hamatocaulis vernicosus*** showing plications at arrow. Photo by Des Callaghan, with permission.

Revolute and Involute Margins

Just as elongate cells of the border permit leaves to become contorted as they dry, the involute (Figure 45-Figure 48) and revolute (Figure 49-Figure 50) margins add structural support to the margin that causes contortions when the leaf dries (Figure 50). This contorted condition is known as **crispate**.

Figure 45. ***Weissia controversa*** that has recently been wet, showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 46. ***Weissia controversa*** dry, showing **crispate** leaf arrangements. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

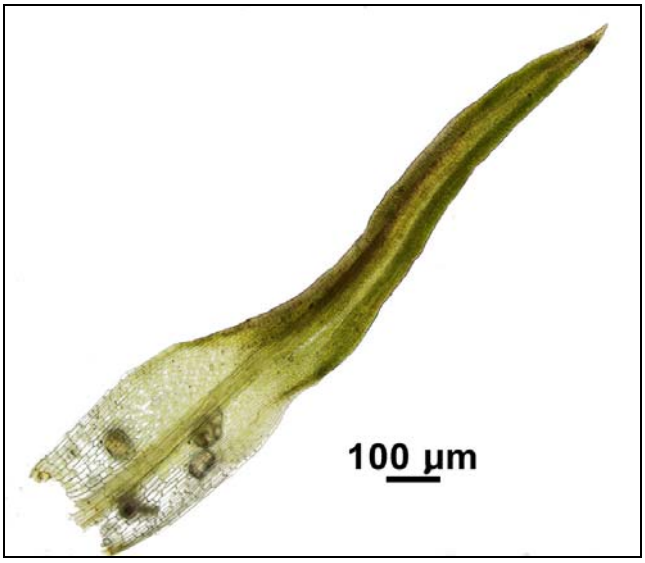

Figure 47. ***Weissia controversa*** leaf showing **involute** margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

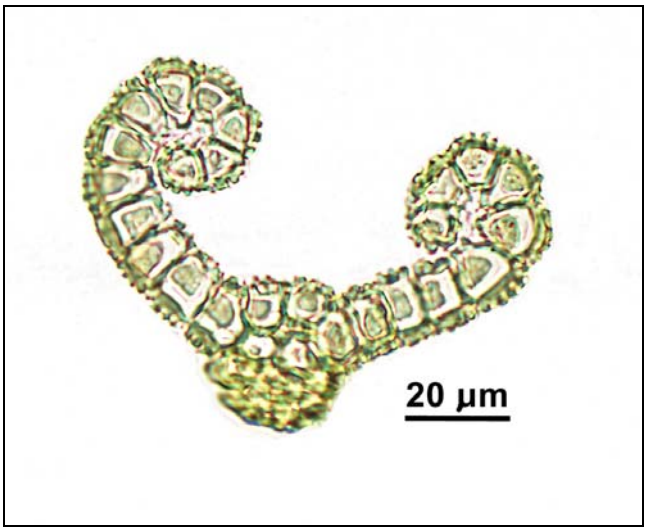

Figure 48. ***Weissia controversa*** leaf cross section showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

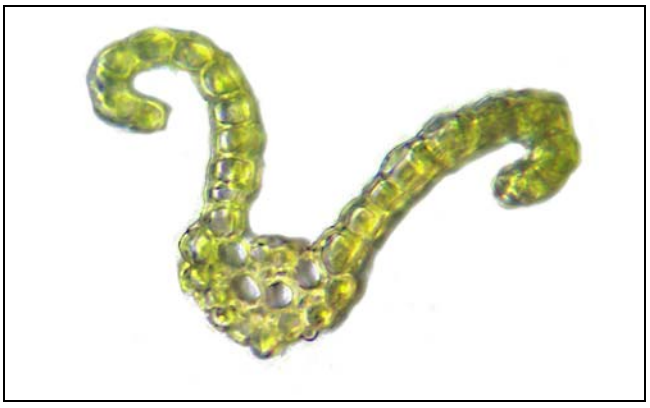

Figure 49. ***Ceratodon purpureus*** leaf cross section showing **revolute** leaf margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

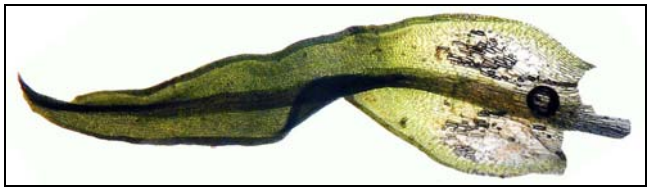

Figure 50. ***Bryoerythrophyllum recurvirostrum*** leaf showing strong costa and **revolute** leaf margin that cause its **crispate** appearance when dry. Photo by Michael Lüth, with permission.

Both **Pottiaceae** and **Grimmiaceae** exhibit crisp, contorted leaves where the lamina is able to shrink and the leaf can roll with marginal rolling increasing as the plants dry (Kürschner 2004). The leaves wind spirally around the stem as they dry, reducing water loss and protecting the chlorophyll and DNA from excessive sunlight. The untwisting of the leaves provides another service – removal of trapped sand particles and other particles held by the leaves. When the lamina folds inward, it reduces desiccation. Kürschner suggests that the shiny costa may increase reflection of sunlight, further reducing desiccation. In these two families that occupy dry, open habitats, parallel evolution has adapted them to their similarly dry niches.

Borders

Borders are usually elongate cells that may be light in color or heavily pigmented. But in some species, the leaf margin may be heavily pigmented with chlorophyll in multiple cell layers. Such is the case in species of ***Pseudocrossidium*** (Figure 51-Figure 54) (Kürschner 2004). These species have marginal cells that form a well developed chlorophyllous region (Figure 52). They are protected by the **revolute** (rolled under; Figure 52-Figure 53) leaf margin that helps to maintain their hydration (Herzog 1926; Kürschner 2004).

So if the costa conducting cells all have protoplasm (**leptoids**), this leaves us with the question of water transport within the leaf. **Leaf borders** with elongate cells such as those in ***Atrichum*** (Figure 55) and the **Mniaceae** (Figure 56) provide benefits similar to those of the costa and seem to speed the movement of water from the base of the leaf to more distal parts, or in some cases from the tip toward the middle, but unfortunately, I have been unable to find any published study to verify this memory. Other roles are discussed in Chapter 7-4.

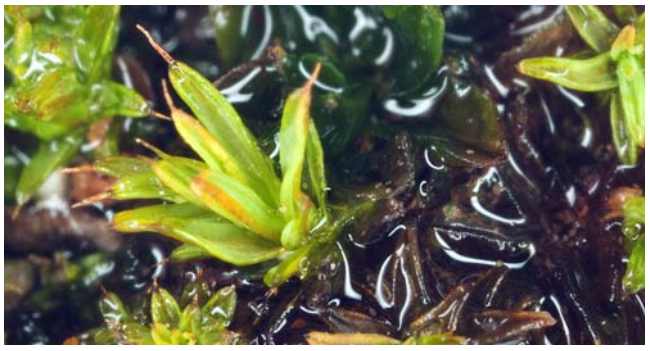

Figure 51. ***Pseudocrossidium crinitum*** hydrated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

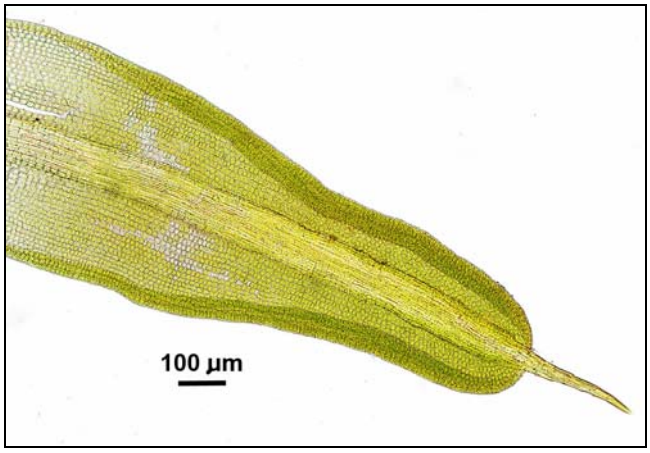

Figure 52. ***Pseudocrossidium crinitum*** underside of leaf showing thickened, revolute, chlorophyllose margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

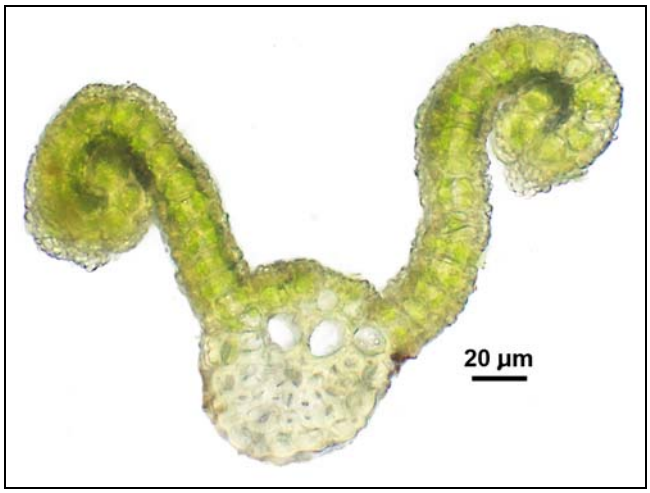

Figure 53. ***Pseudocrossidium crinitum*** leaf cross section showing revolute margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 54. ***Pseudocrossidium revolutum*** showing curled leaves and revolute margins in dry condition. Photo from Proyecto Musgo, through Creative Commons.

Figure 55. ***Atrichum selwynii*** leaf showing border with elongated cells and double border teeth. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 56. ***Plagiomnium affine*** leaf border showing elongate cells compared to wider but shorter leaf lamina cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

It appears that long border cells (Figure 56) are able to move water and facilitate uptake. But they may provide an additional role in the wet to dry state transition of the leaf in at least some taxa (Lowell 1998). When the leaf of ***Atrichum undulatum*** (Figure 57) is wet, the elongate cells of the border are turgid and extend the leaf lamina out into a nearly straight surface. But as the leaf dries, the opposing forces of the drying leaf cells and the border result in the contorted leaf shape that is exhibited by the dry ***Atrichum undulatum*** leaf (Figure 57). The margins roll toward each other and the tip rolls toward the base, creating a "boat" shape. The border acts much like a wire sewn into the edges of a cloth ribbon, but somewhat more flexible.

In ***Atrichum*** (Figure 57) the leaf is **prestressed**; that is, it has a natural dry state that is highly convoluted, but when wet the turgor forces it to become straight (Lowell 1998). Thus, when the leaf dries, the leaf itself contorts into a form that is able to trap and hold water next to the leaf and stem surface. As Lowell describes it, the border is like the party toy that you blow into and it extends straight out, but when it is relaxed, it forms a coil. Species of **Mniaceae** (Figure 58) with borders seem to have similar responses, with the borders causing the leaf margins to curl toward each other, the leaf to become somewhat concave, and the leaf to become contorted.

Figure 57. ***Atrichum altecristatum*** drying (**lower plants**) and moist (**upper plants**). Photo courtesy of Eric Schneider.

Figure 58. ***Plagiomnium*** branch with contorted leaves due to drying. Although this moss has been rewet, it is slow to hydrate and regain its shape. Photo source unknown.

A similar adaptation appears in **Lejeuneaceae** and ***Porella***, where a hyaline row of marginal leaf cells function in water storage (Daniels 1998). Perhaps the same function occurs in some of the mosses such as some ***Fissidens*** (Figure 59-Figure 60) or ***Plagiomnium*** (Figure 56) with well-developed borders. Because of their elongate structure, water can be expected to move more quickly along the border because of fewer end walls to traverse. Yet there seems to be little experimentation to demonstrate that these cells are of any advantage in gaining or moving water to vital parts, or holding water.

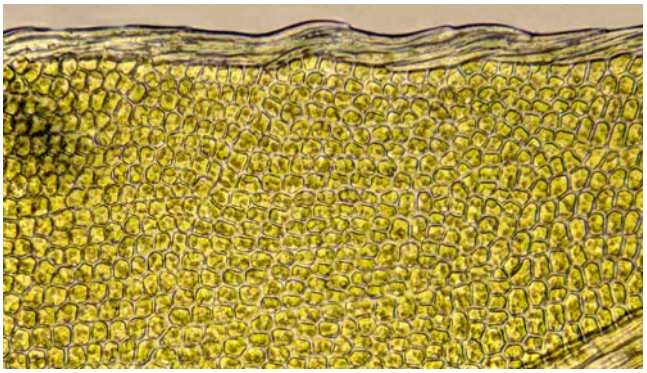

Figure 59. ***Fissidens bryoides*** leaf cells and border, showing elongate border cells. Photo by Dick Haaksma, with permission.

Figure 60. ***Fissidens bryoides*** showing leaves being constricted by their borders. Photo by Michael Lüth, with permission.

Leaf Teeth

Lots of ideas have been presented to suggest the evolutionary significance of teeth in tracheophytes, from deterrents to insects (making the leaf look like something has eaten it, stimulating production of antiherbivore compounds or being spiny) to dripping points for water to help reduce growth of fungi and epiphytes. But what might their value be to bryophytes (Figure 61-Figure 62)?

One interesting observation is that teeth and lobed leaves of deciduous trees are more common in deciduous forests, but they are rare in tropical forests (Baker-Brosh & Peet 1997). Baker-Brosh and Peet hypothesized that they might provide sites for early season photosynthesis. They found that eight species with prominent teeth or lobes did indeed have early season photosynthesis on the margins of the leaves, but not in seven others and none in the four entire-leafed species in the experiments.

Figure 61. ***Mnium spinosum*** leaf showing small, nearly rounded lamina cells compared to the elongate border cells and prominent paired teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Royer and Wilf (2006) noted that toothed leaves of tracheophytes were common in cold climates and that the percentage of toothed leaves correlated negatively with temperature in **mesic** (containing a moderate amount of moisture) environments. They conducted experiments in Pennsylvania and North Carolina, USA, to determine the advantages of the teeth. They found that the physiological activity at the leaf margins was greatest early in the first 30 days of the growing season. And toothed margins were more active in photosynthesis and transpiration than were those of untoothed leaves. They supported the observations of Baker-Brosh and Peet 1997, showing that the leaf margins were more active in leaves from Pennsylvania, which was colder, than those of the California leaves. This strategy maximizes carbon gain during the season when the temperature is limiting but moisture and nutrients are not limiting.

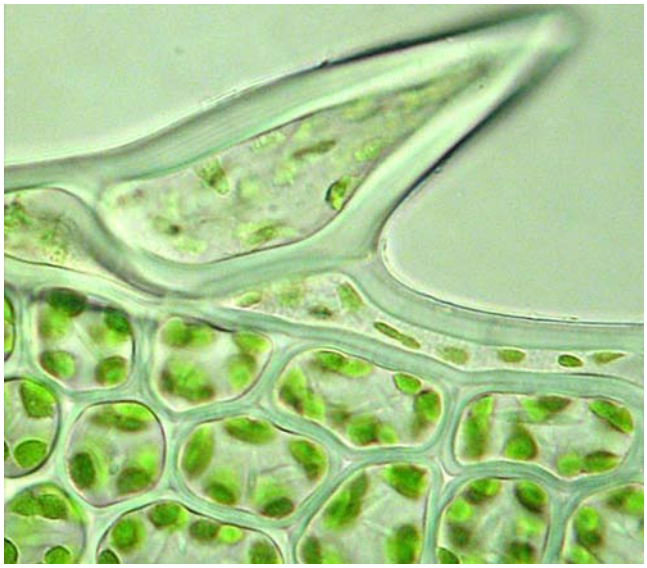

Figure 62. ***Atrichum undulatum*** leaf cells and border showing enlarged tooth with chlorophyll. Photo by Walter Obermayer, with permission.

Obeso (1997) found that spines on the European holly (*Ilex aquifolium*) deterred browsing by ungulates, and that the spines were inducible, decreasing significantly when browsing was prevented for one year.

Another possibility for the adaptive value of teeth is their bearing on water relations. Royer *et al*. (2009) found that among the 227 sites they studied in the Australian subtropical rainforest, both the percentage of species and abundance of toothed species declined from **riparian** (wetlands adjacent to rivers or streams) habitats to ridge-top habitats. Hence, we can rule out any protective value that teeth might have against desiccation. On the contrary, this correlation suggests that teeth could have a role in reducing water in saturated leaves.

Do these tracheophyte models help us to suggest roles for teeth in bryophytes, or are they simply not a detriment to the mosses and liverworts that have them? Do leaf teeth suggest that something has eaten the leaves? We don't know if antiherbivore compounds are inducible in bryophytes, so there may be no disadvantage to having teeth as a warning unless most of the leaves with teeth do have antiherbivore compounds, inducible or not. It seems unlikely that the teeth have any painful effect to deter browsers. And we don't even understand how deciduous tree leaves benefit from teeth in more moist climates.

It is possible that the bryophyte teeth do have a photosynthetic role in spring when new leaves are forming. The apex, especially of acrocarpous mosses, has the most exposure to light, and the marginal parts of the leaves will have the most exposure, so it is possible that they have such a role. But experiments to demonstrate such a benefit are lacking.

Teniolae

The **teniola** is a border-like row of differentiated cells (Figure 63), differing from a true border by being intramarginal (*i.e.* not at the margin). They are more than one cell thick and this condition may extend also throughout the blade portion. These are found in ***Calymperes*** (Figure 64) and function for support, but may also provide water transport (Reese 1993).

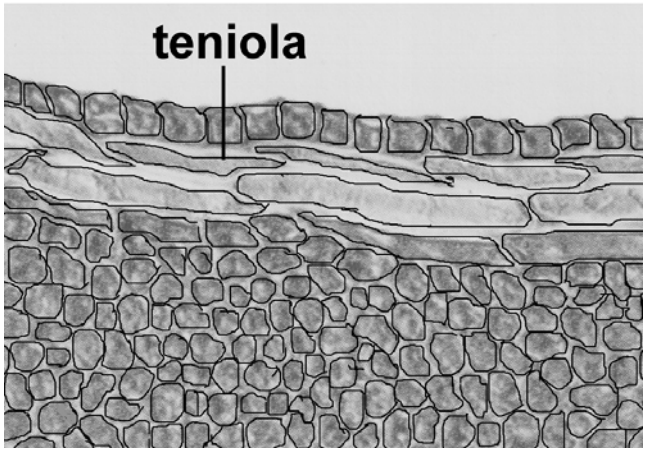

Figure 63. Portion of leaf showing the intramarginal border, the **teniola**. Drawing by Janice Glime.

Figure 64. ***Calymperes motleyi***, member of a genus that has **teniolae**. Photo by Jan-Peter Frahm, with permission.

Costa

The **costa** is the supporting structure for many moss leaves, often also providing an avenue of water transport (Frahm 1985) (Figure 65-Figure 66). It resembles a midrib both in appearance and function (Figure 67). Habitat seems to play some role in its development, although its predisposition to presence or absence is usually genetically determined.

Figure 65. ***Mnium hornum*** showing distinct costa and teeth. Photo by Bob Klips, with permission.

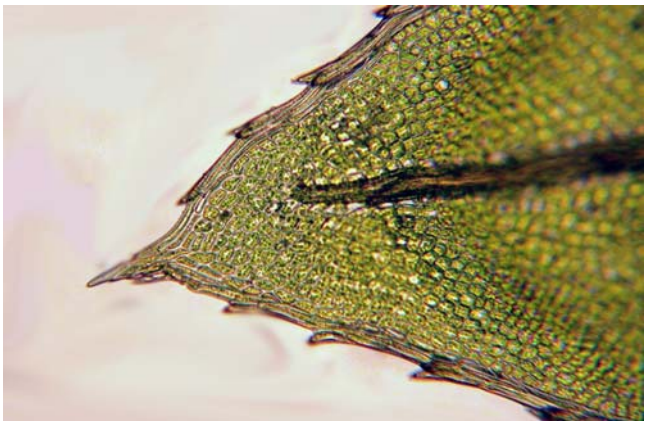

Figure 66. ***Mnium hornum*** leaf showing elongate cells of costa and border. Photo by Bob Klips, with permission.

Figure 67. Cross section of ***Trichodon cylindricus*** showing costa. Photo by Janice Glime.

The costa of some species may be shorter, thinner, and even disappear when it develops in water (Zastrow 1934). For example, the submerged forms of ***Warnstorfia exannulata*** (=*Drepanocladus exannulatus*) (Figure 68-Figure 69) have a costa that only reaches midleaf, whereas the terrestrial forms have a strong costa; similarly, ***Cinclidium stygium*** (Figure 70) normally has a strong costa above water, but when grown submerged it becomes thin and small (Zastrow 1934). When cultured in artificial streams where the leaves were exposed to air, ***Fontinalis novae-angliae*** developed short double costae, although

these are normally absent when it grows submersed (Glime, unpubl.). The broad costa in ***Campylopus*** (Figure 71-Figure 72) not only serves as the photosynthetic organ, but as a water reservoir as well, adding to the possible advantages of growing a costa above water.

Figure 68. ***Warnstorfia exannulata*** branch. Photo from Proyecto Musgo, through Creative Commons.

Figure 69. ***Warnstorfia exannulata*** leaf showing costa typical of emergent leaves. Photo by Kristian Peters, with permission.

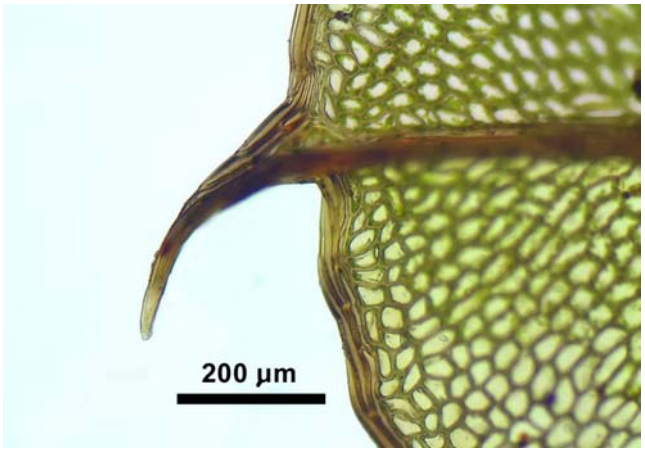

Figure 70. ***Cinclidium stygium*** with leaf tip, costa, and border. Its strong costa indicates that it was grown above water. Photo by Kristian Peters, through Wikimedia Commons.

Figure 71. ***Campylopus lamellinervis*** showing the broad, thickened costa and a tomentum on the stem that absorbs moisture. Photo by Michael Lüth, with permission.

Figure 72. Leaf cross section of ***Campylopus flexuosus*** showing broad costa with cells that have water-holding capacity as well as photosynthetic capacity. Photo by Michael Lüth, with permission.

Guerra *et al.* (1992) considered **nerve enlargement** to be an adaptation to the xeric environment, providing stiffening that supports the leaf during desiccation. Bell (1982) suggested that it also might retain water.

Stereids

In the stem, **stereids** are thick-walled cells that contain living protoplasm and have been compared to xylem parenchyma cells (Hébant 1970). In leaves, they form ribs on one or both sides of the costa (Figure 73) and may function as protection against desiccation (Frahm 1985). They occur in a variety of families, including **Dicranaceae** (Figure 74) and **Pottiaceae** (Figure 75-Figure 76).

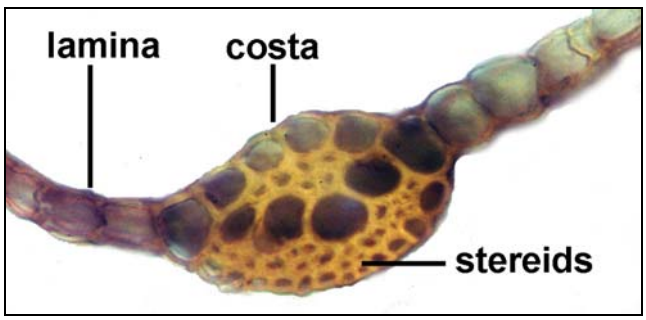

Figure 73. ***Trichostomum tenuirostre*** (moss) leaf cross section showing stereids. Photo by Janice Glime.

Figure 74. ***Dicranum scoparium*** (**Dicranaceae**) leaf cross section. This leaf has few sclereids but has relatively large conducting cells, in this case smaller than the leaf lamina cells. Photo from Botany website, University of British Columbia, Canada.

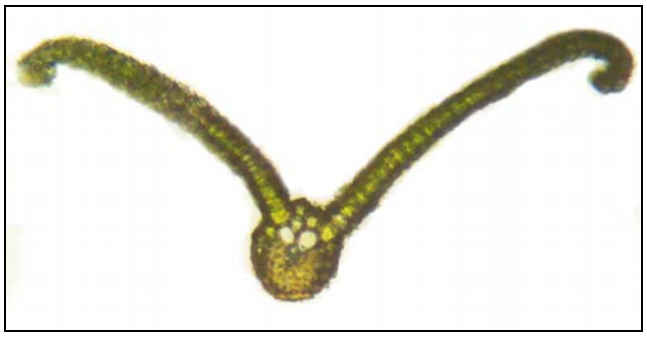

Figure 75. ***Syntrichia inermis*** (**Pottiaceae**) leaf cross section. Note the enlarged costa with stereid cells on the bottom and conducting cells near the top. In this case, the lamina cells are covered with papillae that may help in water intake, a function thus far demonstrated for only one species. More likely they channel the water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 76. ***Syntrichia princeps*** (**Pottiaceae**) leaf cross section showing costa with stereids (pinkish color on lower portion) and large leptoids. Photo by Paul S. Wilson.

It appears that the structure of the costa can have adaptive value relating to moisture conditions. Those ***Campylopus*** taxa surviving habitats with changeable conditions have well-developed costal stereids (Frahm 1985). Frahm found that dorsal costal **lamellae** (Figure 95) aid in water uptake, whereas the ventral costal stereids (Figure 77) common among ***Campylopus*** species help to reduce desiccation. ***Campylopus savannarum*** survives its savannah habitat with the aid of such stereids, whereas ***Campylopus*** taxa occurring on wet cliffs, dripping rocks, and swamps lack stereids (Figure 78).

Figure 77. ***Campylopus flexuosus*** leaf cross section showing ventral (lower) stereids. Photo by Amelia Merced, Duke Herbarium.

Figure 78. ***Campylopus tallulensis*** leaf cross section showing thin-walled ventral costal cells typical of the more humid mountainous regions. Photo by Amelia Merced, with permission.

Lamellae

The term **lamella** shares the same root word as laminate and refers to layers, in this case vertical stacks of cells that form rows, often reaching the length of the leaf (Figure 82, Figure 83). They may cover the costa, the blade, or a liverwort thallus. These rows are arranged in such a way that they somewhat resemble a book that has just been opened and laid to rest, with its pages still parting and standing upward from the middle. Some of the most **xerophytic** (referring to plants of dry habitats) mosses, such as ***Aloina*** (Figure 79), have branched filaments over the costa, giving it a **succulent** (fleshy) appearance; ***Crossidium*** (Figure 80-Figure 81) achieves a similar effect with dense filamentous outgrowths from the costa in the upper half of the leaf.

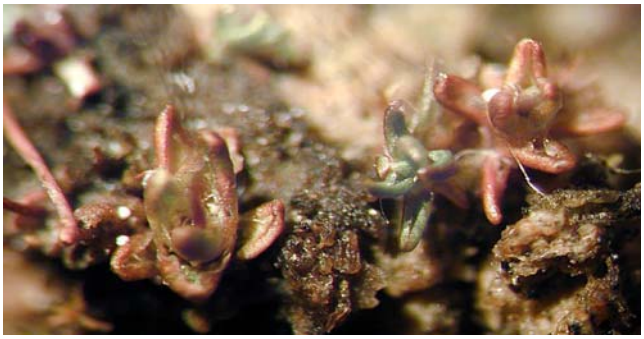

Figure 79. ***Aloina brevirostris***, illustrating the succulent appearance caused by the numerous filaments on the costa. Photo by Michael Lüth, with permission.

Figure 80. ***Crossidium crassinerve*** with filaments on leaf costae. Photo by Michael Lüth, with permission.

Figure 81. ***Crossidium aberrans*** leaf showing filaments on costa. Photo by Michael Lüth, with permission.

Members of the **Polytrichaceae**, such as ***Polytrichum*** and ***Dawsonia***, which are all **endohydric** (having internal water transport), have vertical lamellae (Figure 82, on their leaves that provide capillary spaces and create dead air spaces that can reduce water loss across the broad surface of these atypically large moss leaves (Figure 82-Figure 85). In addition, some species [***Polytrichum hyperboreum*** (Figure 86-Figure 87), ***P. piliferum*** (Figure 88-Figure 89), ***P. juniperinum*** (Figure 90-Figure 91)] have the edge of the leaf **lamina** (flattened part of leaf not including costa or border) rolled over the lamellae, creating an internal structure somewhat like the **palisade mesophyll** (columnar cells of inner leaf tissue) of a flowering plant, with the lamina behaving in some ways like an epidermis. The leaves have the additional ability to flex like a hinge when water fills the thin-walled leaf base cells (van Zanten 1975), causing the leaves to be spread lengthwise away from the stem under moist conditions but be straight or curved around the stem when dry (Figure 2). Such behavior retards water loss and protects the chlorophyll during dry periods, while permitting maximum use of light during wet periods.

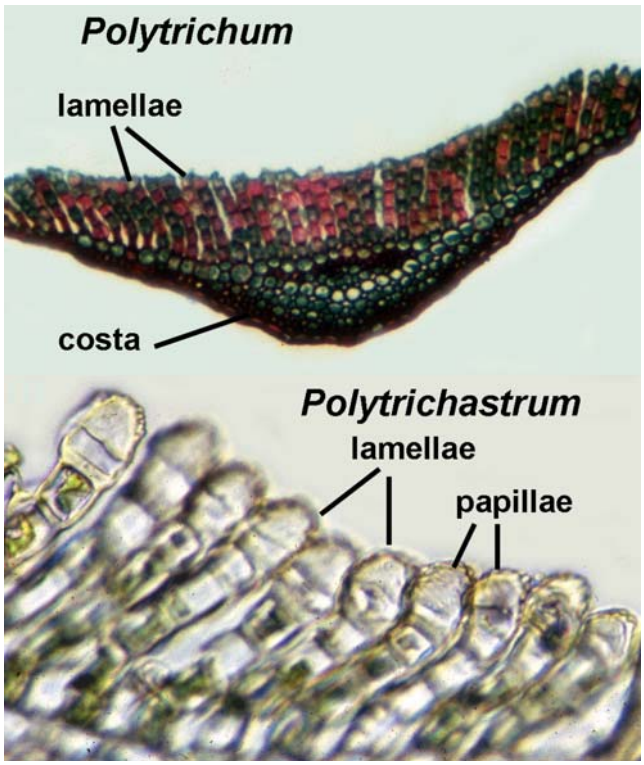

Figure 82. Cross sections of lamellae of **Polytrichaceae**. **Top:** stained section of ***Polytrichum***. **Bottom:** ***Polytrichastrum alpinum*** with papillose terminal cells on the lamellae. Photos by Janice Glime.

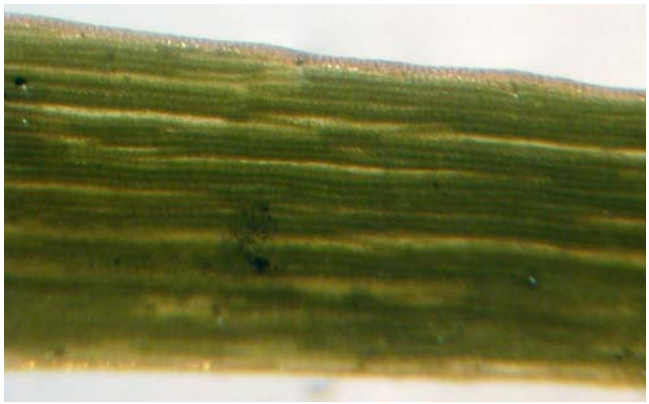

Figure 83. Lamellae on leaf of ***Polytrichum ohioense***, viewed down onto leaf surface at 100X. Photo courtesy of John Hribljan.

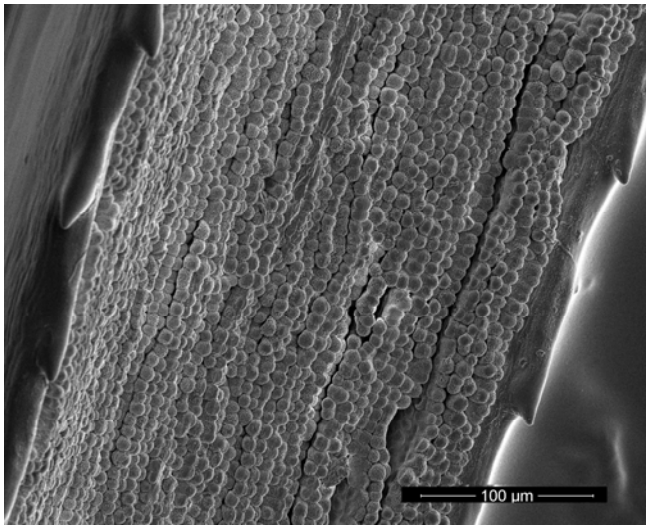

Figure 84. SEM of ***Dendroligotrichum squamosum*** (**Polytrichaceae**) showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

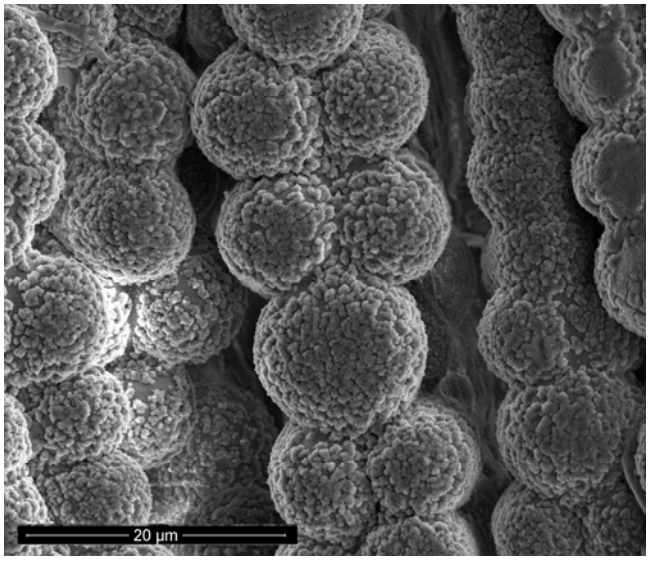

Figure 85. SEM of ***Dendroligotrichum squamosum*** leaf showing terminal cells of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 86. ***Polytrichum hyperboreum*** showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

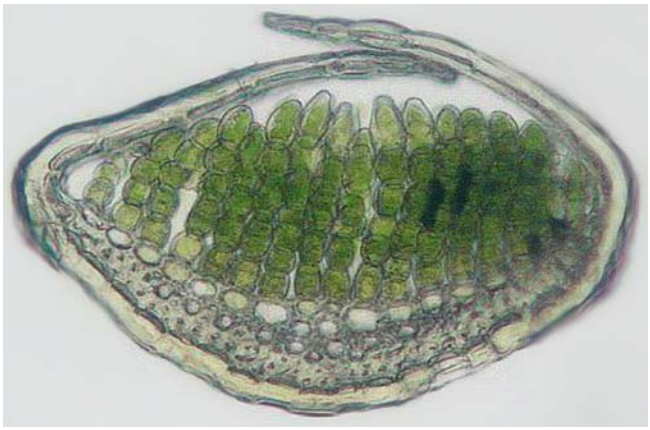

Figure 87. ***Polytrichum hyperboreum*** leaf cross section showing lamina folded over lamellae. Photo by Michael Lüth, with permission.

Figure 88. ***Polytrichum piliferum*** showing leaf lamina rolled over the lamellae. Photo from Botany Department website, University of British Columbia, Canada, with permission.

Figure 89. ***Polytrichum piliferum*** leaf cross section showing leaf lamina rolled over the lamellae. Photo from Botany website, University of British Columbia, Canada, with permission.

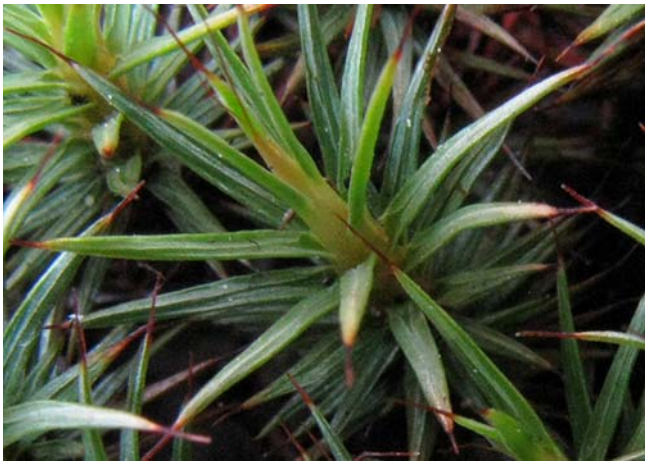

Figure 90. ***Polytrichum juniperinum*** showing leaf lamina rolled over leaf lamellae. Overlap can be seen easily near leaf bases where the overlap is incomplete, permitting water to enter the basal cells. Photo by Janice Glime.

Figure 91. ***Polytrichum juniperinum*** leaf cross section showing leaf lamina rolled over leaf lamellae. Photo by John Hribljan, with permission.

In ***Pilopogon laevis*** (Figure 92) the costa is ribbed on the back of the leaf; in ***P. peruvianus*** (Figure 93-Figure 94) it has 3-4-cell-high lamellae on the back of the leaf, adapting this species to its dry coastal desert habitat. Likewise, ***Campylopus pilifer*** (Figure 95) has similar lamellae and prefers such dry habitats as rocks, soil-covered boulders, and gravel. On the other hand, ***C. introflexus*** (Figure 96) has only 1-2-cell-high lamellae and lives on humus, wet sand, and peat.

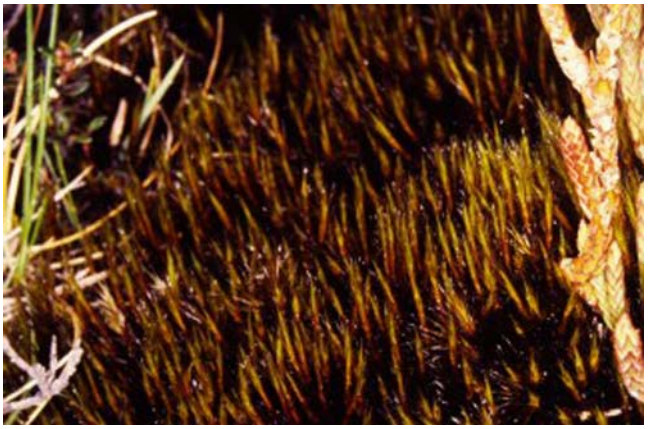

Figure 92. ***Pilopogon laevis***, a species with a ribbed costa. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Pilopogon peruvianus*** in its desert habitat. Photo by Michael Lüth, with permission.

Figure 94. ***Pilopogon peruvianus*** leaf cross section showing 3-4 cell high lamellae. Photo by Michael Lüth, with permission.

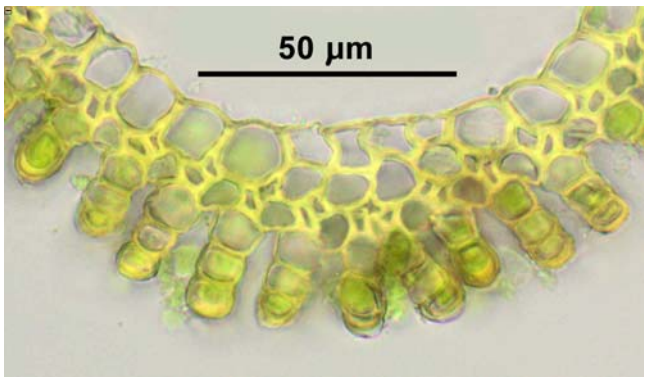

Figure 95. ***Campylopus pilifer***, a plant of rocks and gravel, leaf cross section showing deep lamellae. Photo by Amelia Merced, Duke Herbarium, with permission.

Figure 96. ***Campylopus introflexus***, a plant of humus, wet sand, and peat, leaf cross section showing shallow lamellae. Photo by Gilles Bailly, through Creative Commons.

Although Frey and Kürschner (1991) found a correlation between costal lamellae and increasing aridity, the lamellae of ***Polytrichum*** seem not to be so much an adaptation to prevent water loss as to provide for additional surface area [2.4-fold in ***Polytrichum commune*** (Figure 97-Figure 98)] and gas exchange during photosynthesis (Thomas *et al.* 1996). Proctor (1979a, b) and Thomas *et al.* (1996) described wax on the terminal cells of the lamellae of ***Polytrichum*** and attributed to this wax the repulsion of water, preventing it from entering between the lamellae. Perhaps lamellae are adapted to increasing gas exchange and are more important in water retention or repulsion than in absorption, at least in some species.

Figure 97. ***Polytrichum commune*** leaves with waxy surface that keeps water out of the lamellae. Photo by James K. Lindsey, with permission.

The genus ***Atrichum*** (**Polytrichaceae**) also has shallow to deep lamellae, and these have been used to justify separation into different species. The lamellae shown in Figure 99-Figure 101 fall within ***Atrichum undulatum*** var. ***undulatum***, but any lamellae more than 4 cells high would indicate a different variety (Crum 1983), or species (The Plant List 2010).

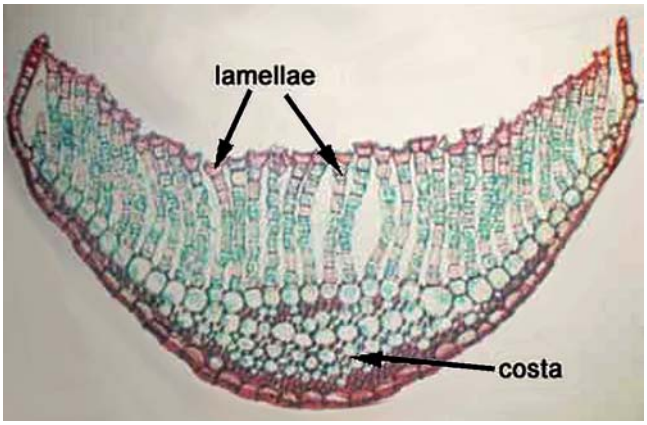

Figure 98. ***Polytrichum commune*** leaf cross section with lamellae showing terminal cell with different stain from other lamellae cells, perhaps due to the presence of wax. Photo from Botany website, UBC, with permission.

Figure 99. ***Atrichum undulatum*** leaf showing leaf lamellae and border with teeth. Photo by Walter Obermayer, with permission.

Figure 100. ***Atrichum undulatum*** leaf (costa) cross section showing small, thick-walled stereids, large transparent conducting cells, and lamellae 3-4 cells high. Photo by Walter Obermayer, with permission.

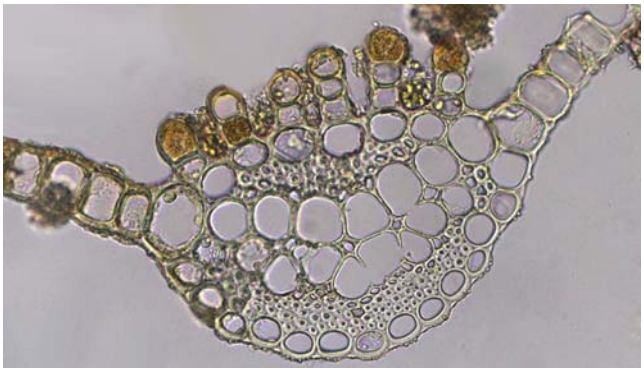

Figure 101. ***Atrichum undulatum*** leaf (costa) cross section showing small, thick-walled stereids above and below the large, transparent conducting cells. Lamellae are on top of the costa and are only 2-3 cells high. Photo by Walter Obermayer, with permission.

Lobules and Storage Organs

Liverworts have an evolutionary history that separates some of the major groups by their water relations (Heinrichs *et al*. 2005). In the **Jungermanniidae**, two clades split. The **Porellales** are predominantly epiphytes that have specialized **lobules** (Figure 102) or water sacs and **endosporous** protonemata. The **Jungermanniales** (Figure 103) are frequently terrestrial, lack water sacs, and normally develop **exosporous** protonemata.

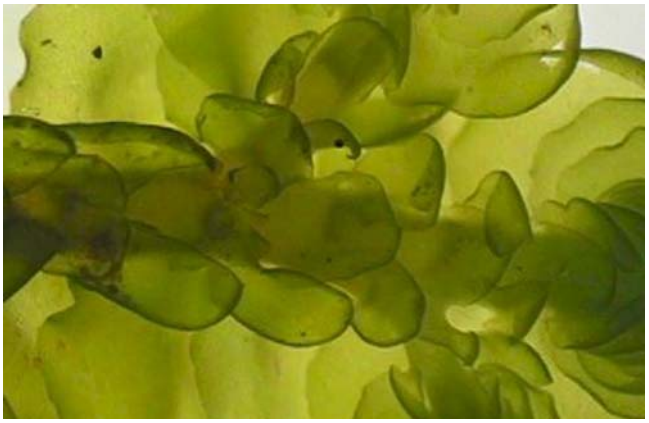

Figure 102. Ventral side of ***Porella platyphylla*** showing underleaves along stem and lobules on each side of them. Photo by Paul Davison, with permission.

Figure 103. ***Lophozia wenzelii***, a member of the **Jungermanniales,** showing the absence of lobules. Photo by Des Callaghan, with permission.

Daniels (1998) has compared leafy liverworts growing in a variety of habitats. **Xerophytic** (dry habitat adapted) taxa such as ***Frullania*** (Figure 104) have helmet-shaped leaf **lobules** and ***Radula*** (Figure 105) has a saccate lobule, both functioning for water storage. ***Porella*** (Figure 102), capable of both an **epiphytic** (living on plants) and a **saxicolous** (living on rock) habit, has leaf folds underneath (lobules) and large underleaves. Liverwort plants in the humid rainforests such as those in the **Lejeuneaceae** (Figure 106-Figure 108) have smaller lobules than those growing in drier, more exposed habitats (Cornelissen & ter Steege 1989; Gradstein 1995). Such structures help to hold water in capillary spaces in the absence of multiple rows of leaves. Some aquatic invertebrates, especially rotifers, live in these watery lobules (see Volume 2, Chapter 4-5 on Rotifers). It is likely that the pockets of ***Fissidens*** (Figure 21-Figure 24, Figure 37) may have similar water-holding functions.

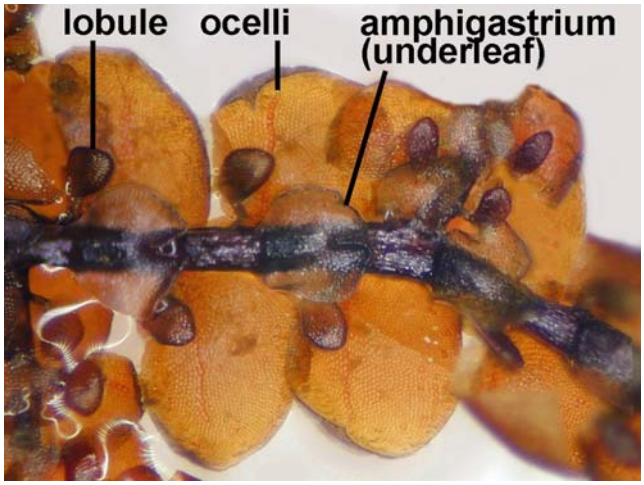

Figure 104. ***Frullania tamarisci*** showing lobules. Photo by Michael Lüth, with permission.

Figure 105. ***Radula*** from the tropics with saccate lobules (**arrows**). Photo by Michael Lüth, with permission.

Figure 106. **Lejeuneaceae** epiphylls from Panama. Photo by Janice Glime.

Figure 107. ***Lejeunea patens*** showing small lobules. The upper three have air bubbles trapped in them. Photo by Jan-Peter Frahm, with permission.

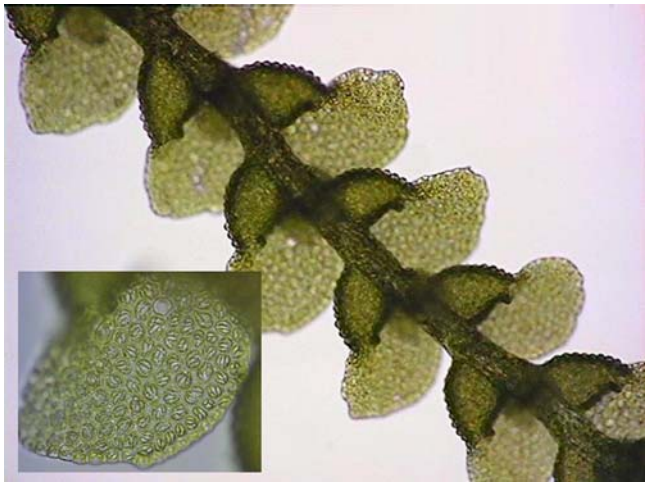

Figure 108. ***Cheilolejeunea evansii*** branch showing ventral lobules. Photo by Paul Davison, with permission.

Hair Points

Hair points are common on leaves of xerophytic mosses, including species of ***Campylopus*** (Figure 109-Figure 110), ***Grimmia*** (Figure 111), ***Schistidium*** (Figure 112-Figure 113), ***Hedwigia*** (Figure 134), and ***Syntrichia*** (Figure 114). As discussed earlier, Loeske, in 1930, demonstrated that in ***Schistidium apocarpum*** (Figure 112-Figure 113) hair points are actually lost when the mosses are kept in damp air or deep shade. Proctor (1979a) and Kürschner (2004) consider these hairs to be organs that reflect some of the solar radiation, thus reducing energy absorption, temperature, and evaporation. But they reduce water loss more directly as well; hair points on ***Syntrichia intermedia*** (Figure 114) and ***Grimmia pulvinata*** (Figure 111) reduce the boundary layer conductance by about 20-35% in experiments (Proctor 1980). Not only does this thicker boundary layer trap stagnant air, thus reducing evaporation loss, but it increases the distance from the leaf surface to the surrounding air, thus decreasing the diffusion gradient (Proctor 1982).

Figure 109. ***Campylopus introflexus*** showing dry hair tips. Compare to Figure 110. Photo by Michael Lüth, with permission.

Figure 110. ***Campylopus introflexus*** showing hair tips that have collected moisture from the atmosphere. Photo by Michael Lüth, with permission.

Figure 111. ***Grimmia pulvinata*** showing the long hairs that reduce the boundary layer conductance and trap atmospheric moisture. Photo by Michael Lüth, with permission.

Figure 112. ***Schistidium apocarpum*** exhibiting the lack of hair points typical of this species when it is grown in wet or shaded habitats. Photo by Christophe Quintin, through Creative Commons.

Figure 113. ***Schistidium apocarpum*** exhibiting the leaf hair points that develop when the plants are in dry areas. Photo by Christophe Quintin, through Creative Commons.

Hair points may also help in trapping and absorption of water vapor from fog and dew (Figure 109-Figure 110). Dry tips can reflect sunlight (Figure 109), reducing water loss (Kürschner 2004).

Figure 114. ***Syntrichia intermedia*** demonstrating prominent hair points. Photo by Jan-Peter Frahm, with permission.

As suggested by the example of ***Campylopus introflexus*** (Figure 109-Figure 110), hair points can help in collecting moisture from the air as well (Figure 110). Shaun Russell has described to me that in African highlands the mosses act as tiny collectors that trap moisture from the fog. This is often their only source of water for an entire year. Chang and coworkers (2002) have measured the water available to epiphytes in fog (Table 2) and in precipitation in a subtropical montane forest in Taiwan. In a one-year study, they found that the fog endured for a mean of 4.7 hours per day at its low in the summer to 11 hours per day the rest of the year, reaching nearly 15 hours per day in November. Furthermore, it contributed more than 50% of the nutrient ions reaching the bryophytes.

Table 2. Absorption rate of fog in dominant epiphytes during a single dense fog event on 24 February 2001 at Yuanyang Lake, Taiwan. From Chang *et al*. (2002).

Species	absorption rate g H_2O gdw^{-1} h^{-1}
Bazzania fauriana	1.28
Bazzania sp. 2	0.90
Pleurozia acinosa	0.67
Mastigophora diclados	0.59
Schistochila acuminata	0.58
Dicranoloma blumii	0.42
Scapania sp. 1	0.38
Bazzania sp. 1	0.23

Zhang *et al*. (2009) considered the effect of dew as an important moisture source in the Gurbantunggut Desert, Northwestern China. They measured dew quantities with micro-lysimeters and demonstrated the increase in dew deposition as the crust grew larger. Mosses had the highest deposition compared to that of lichen crusts, cyanobacterial crusts, and bare sand ($p < 0.05$). Interestingly, the retention time for the moisture gained from dew did not follow this pattern. Instead, it was held longest by sand, followed by the cyanobacterial crust, moss crust, and lichen crust, in that order.

Tao and Zhang (2012) further examined the function of hair points in the desert moss ***Syntrichia caninervis*** (Figure 115). The hair points in this case comprised only about 4.8% of the shoot weight, but they were able to increase the absolute water content by 24.9%. And, during dehydration, those moss samples with hair points always

had a higher water content than did those without. Furthermore, the shoots with hair points took 20 minutes longer to become completely dehydrated. And of course there was greater dew accumulation on the shoots with leaf hair points, increasing the dew on the crusts by 10.3%. Following short simulated rainfall events, the evaporation of water from the crusts was always slower when the leaves had hair points in contrast to the rapid loss of water trapped from dew (Zhang *et al*. 2009).

Yuan Ming Zhang's research team filmed the events following application of a drop of water on the hair points of ***Syntrichia caninervis*** (Figure 115). The water moved quickly down the hair point and was absorbed by the leaves within seconds. Like a fine wire, the hair tips serve as a conduit for the water. This mechanism permits these mosses to extract water from dew or fog, and to benefit from rapid absorption of the first few drops of rain, maximizing its period of hydration. Zhang *et al*. (2011) supported the significance of this rapid rewetting. In lab experiments they showed that within the first minute the photosynthetic yield (F_v/F_m) recovered to 90% of its rate after 30 minutes. Cytological changes occurred rapidly, indicating no damage to membranes or organelles. This rapid recovery makes it possible for it to use the water collected by the hair points from fog, dew, rain, and melting snow for immediate recovery, making it possible to attain positive photosynthetic gain in its desert ecosystem.

Figure 115. ***Syntrichia caninervis***, a desert crust moss with hair points that are important to the hydration of the crust. Photo by John Game, through Creative Commons.

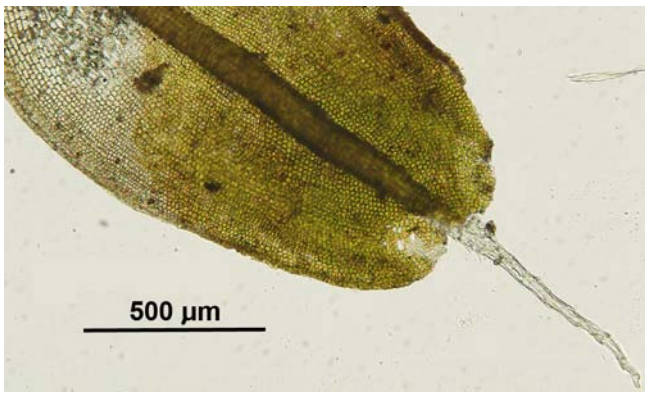

Figure 116. ***Syntrichia caninervis*** leaf showing awn. Photo by Yuan Ming Zhang.

Duration of the rainfall or dew fall event is important. Proctor (2004) found that in ***Grimmia pulvinata*** (Figure 111), dew fall did not enter the moss sufficiently to rehydrate it. Could these hair points prevent wetting and drying cycles that are too frequent for adequate repair of dehydration damage in mosses regularly subjected to hot, dry days? Is this a mechanism to prevent the leaf from becoming hydrated at a time when it will dehydrate again within hours? This is reminiscent of the dormancy mechanism in desert seeds wherein a chemical must be washed off before the seed will germinate. This keeps the seed from germinating unless there is enough rainfall to sustain the young seedling until it reaches a size where it can survive. In these mosses, it requires a rainfall that will hydrate the moss long enough for it to repair the damage of desiccation and make a positive photosynthetic gain before becoming dehydrated again.

Nucleation

It appears that bryophytes are good nucleators. This is a phenomenon in which a small object, known best from bacteria and proteins, causes the formation of ice around itself. Moffett *et al*. (2009) suggest that this phenomenon is widespread among bryophytes. Nucleation occurs when the difference in vapor pressure over ice and water is at or close to the maximum. At these temperatures, typically -8 to -18°C, ice grows at the expense of supercooled water. Moffett *et al*. suggest that the nucleation ability permits the bryophytes to collect water from fog, dew, and cloud water. It is interesting to note that airborne bryophytes may use this nucleation to initiate precipitation.

Papillae

Papillae in bryophytes are small projections from cells, especially common in the **Pottiaceae** (Figure 117-Figure 118). Kou *et al*. (2014) attempted to limit the confusion of many terms in their descriptions by providing four terms to describe them: simple, forked, branched, and pedicellate.

Papillae can both facilitate rapid water uptake (Proctor 1979a; Longton 1988; Kürschner 2004) and accelerate water loss (Pressel *et al*. 2010). Species that benefit from these papillae must, as a consequence, shut down under drying conditions. This is consistent with the role of surface waxes (discussed in Chapter 7-4b of this volume). The thick surface waxes of tracheophytes are usually associated with conditions of drying. In bryophytes, however, they are often characteristic of species from constantly flowing aerated water or other places where water logging depresses gas exchange (Pressel *et al*. 2010). In other words, often they are important for their **hydrophobic** (water-repelling) nature.

The role of papillae, those little bumps and extensions on cell walls (Figure 118), has been controversial for a long time, but their common appearance on bryophytes of dry habitats cannot be ignored. Nevertheless, Loeske (1926) points out that papillae are also found in a number of wetland and aquatic taxa, including ***Dichodontium pellucidum*** (Figure 119-Figure 120), ***Philonotis*** (actually **prorate** cells – end walls overlap and protrude; Figure 121-Figure 122), ***Aulacomnium palustre*** (Figure 123-Figure 124), ***Helodium blandowii*** (Figure 125-Figure 126), and ***Paludella*** (Figure 127). Loeske observed that the papillae

are maintained in a number of species through a wide range of wet to dry habitats. On the other hand, these taxa are common in wet meadows, lake shores, and other wet habitats where they may periodically be dry while being exposed to high sunlight, suggesting that the papillae may be of value under those exposed conditions.

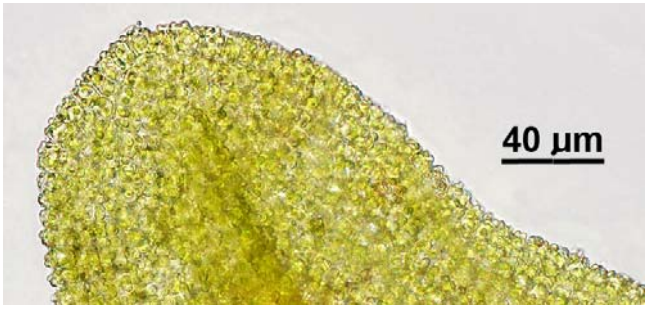

Figure 117. ***Barbula convoluta*** leaf cells showing papillae (especially visible as tiny projections along the margins). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 118. ***Chrysoblastella chilensis*** leaf cross section showing papillae. This leaf is well endowed with stereids in the costa. Photo by Juan Larrain, with permission.

Figure 119. ***Dichodontium pellucidum*** showing dull, waxy look that results from surface papillae. Photo by Jan-Peter Frahm, with permission.

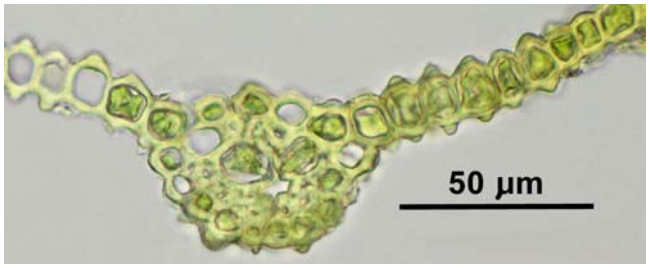

Figure 120. ***Dichodontium pellucidum*** leaf cells in cross section showing papillae. Photo by Amelia Merced through Duke University Plant Biology website, with permission.

Figure 121. ***Philonotis fontana*** exhibiting dull appearance resulting from **prorate** cells. Photo by Malcolm Storey, through Creative Commons.

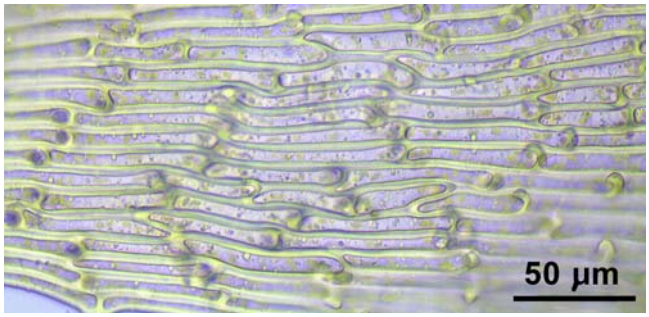

Figure 122. ***Philonotis fontana*** leaf lamina showing **prorate** cells that have an appearance similar to papillae. Photo by Kristian Peters, through Creative Commons.

Figure 123. ***Aulacomnium palustre***, wetland moss with papillae. Photo by David T. Holyoak, with permission.

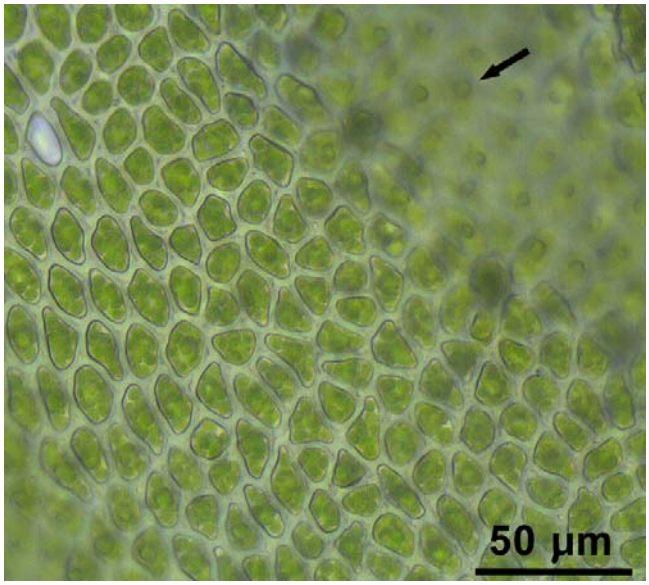

Figure 124. ***Aulacomnium palustre*** leaf lamina showing papillae, best seen in the upper right corner at arrow. Photo by Kristian Peters, through Creative Commons.

Figure 125. ***Helodium blandowii***, a moss that feels "crunchy" due to papillae. Photo by J. C. Schou, through Creative Commons.

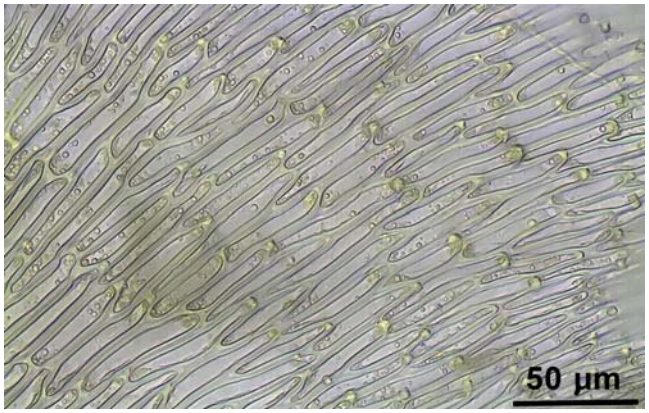

Figure 126. ***Helodium blandowii*** leaf with **prorate** cells. Photo by Kristian Peters, with permission.

Figure 127. ***Paludella squarrosa***, emergent in full sun. Photo by Michael Lüth, with permission.

Some papillae are quite decorative, adorning species that typically live on limestone rocks or other highly desiccating habitats. ***Encalypta ciliata*** (Figure 128-Figure 130) has branched papillae and lives on limestone rocks and other dry locations.

Figure 128. ***Encalypta ciliata*** in a hydrated state, showing the nearly translucent appearance of the leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 129. ***Encalypta ciliata*** in a dry state, showing the dull surface of the contorted leaves. Photo by Li Zhang, with permission.

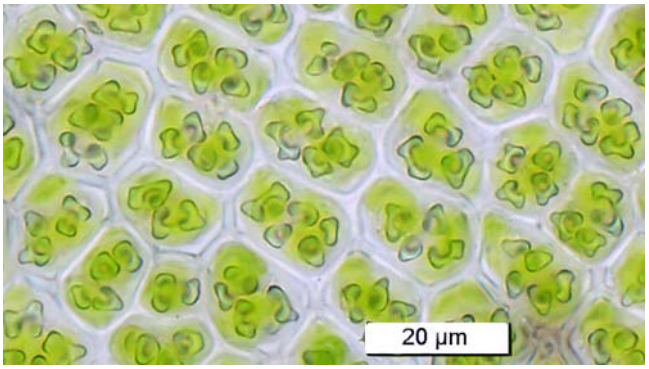

Figure 130. ***Encalypta ciliata*** leaf cells with multiple papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Proctor (1979a, 1984, also Longton 1988) described the interstitial spaces between papillae as forming a capillary conducting system that is capable of rapid water movement, as we might expect in ***Tortula muralis*** (Figure 131-Figure 132). (See also the chapter on Leaf Strategies – Cuticles and Waxes in this volume.) But papillae may be most important in altering the boundary layer and creating a dead space that reduces water loss. Both of these ideas, as well as their role in deflecting UV light, remain to be tested.

Figure 131. ***Tortula muralis*** leaf cross section showing the multiple papillae on each cell. Photo from Botany Department website, University of British Columbia, with permission.

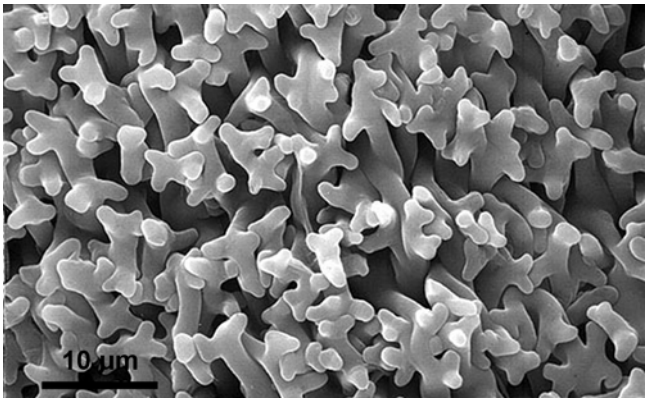

Figure 132. SEM of papillae on ***Tortula muralis***, illustrating the type of channelling described by Proctor (1984). Photo with permission from Botany 321 website, <www.botany.ubc.ca/bryophyte/LAB8.htm>, with permission.

Hedwigia ciliata (Figure 133-Figure 134) is a moss that has white tips on its leaves, presumably protecting the underlying leaves from sun damage. But we need to examine the role of these tips in water uptake as well. The leaf and awn cells are heavily endowed with papillae that give the leaves a waxy appearance despite the absence of waxes.

Figure 133. ***Hedwigia ciliata*** with hyaline tips and awns on leaves. Photo by Michael Lüth, with permission.

Figure 134. Hyaline hair tip on the leaf of ***Hedwigia ciliata***. Note the numerous papillae on these **awn** (hair tip) cells as well as on the **lamina** cells. Photo by Janice Glime.

At least some leaf papillae (***Andreaeobryum macrosporum***, Figure 135) are constructed in such a way that they provide a channel for the uptake of water (Crandall-Stotler & Bozzola 1990, 1991). This channel is within each papilla and is different from the channels formed between the papillae (*cf.* Proctor 1984). SEM observations indicate the channel within the papilla facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991). So far, this channel has not been demonstrated in any other species.

So how can papillae function both for water absorption and water loss, and why would evolution tolerate such a seeming contradiction? Pressel *et al*. (2010) may have answered this question. They found that in ***Rhacocarpus purpurascens*** (Figure 136), the **trilamellate** (having 3 layers) walls have a porous outer layer that permits rapid uptake of water, whereas its cuticle-like layer is highly hydrophobic and prevents water-logging. Could it be that the papillae of bryophytes create that space needed to prevent water-logging? But Pressel and coworkers contend that papillae in ***R. purpurascens*** accelerate water loss,

resulting in a metabolic shutdown when the plants are water-stressed. With the wide variety of shapes, sizes, and density of papillae among the bryophytes, it is still possible that some have the ability to prevent water-logging during the critical periods when the plants are wet in normally dry habitats. If this ability exists, it may be of considerable importance in at least some cases.

Figure 135. ***Andreaeobryum macrosporum***, a moss for which papillae are known to aid in uptake of water through a channel in the papilla. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 136. ***Rhacocarpus purpurascens*** showing shiny leaves. Photo by Michael Lüth, with permission.

One such species is the desert moss, ***Syntrichia caninervis*** (Figure 115, Figure 137-Figure 139). When Wu *et al*. (2014) compared absorption of rhizoids to that of leaves, the leaves were clearly the greater absorptive organs. They tested absorption by dropping water onto the upper and lower leaf surfaces, both of which have C–shaped papillae (Figure 137) (Zheng *et al*. 2010). Wu and coworkers found that the adsorption by the papillae is so rapid that they could not determine the leaf angles. They concluded that in this case the papillae are **superhydrophilic** (having a highly efficient water absorption mechanism). The spaces between the papillae form microcapillary spaces that serve as an efficient conducting system (see also Koch *et al*. 2008).

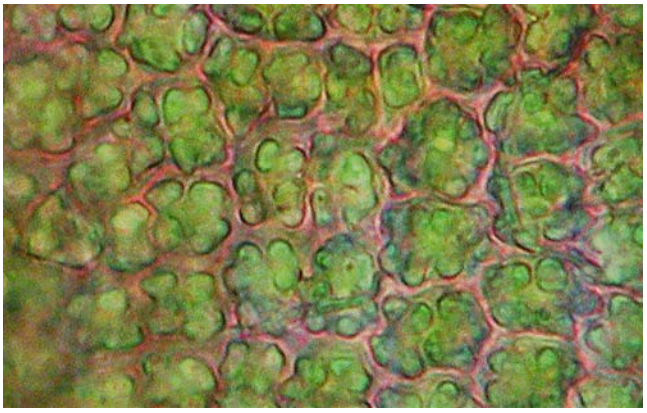

Figure 137. ***Syntrichia caninervis*** leaf papillae. Photo by Michael Lüth, with permission.

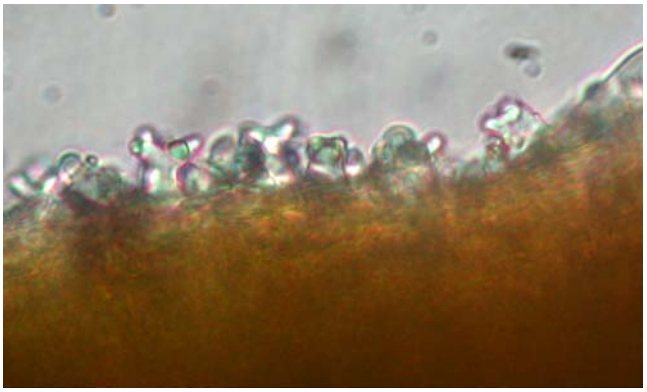

Figure 138. ***Syntrichia caninervis*** side view of leaf papillae that appear C-shaped from above. Photo by Terry McIntosh, with permission.

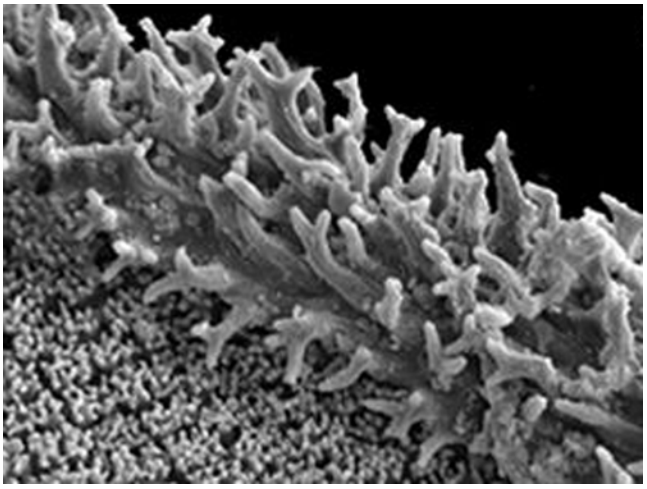

Figure 139. ***Syntrichia caninervis*** var. ***caninervis*** showing long papillae on costa and smaller ones on cells. Photo by M. T. Gallego.

The only thing that seems clear about papillae is that our understanding of them is not clear. It is likely that papillae cannot be lumped into one function, but that shapes, structure, and arrangement may create different capabilities, and these must coordinate in various ways with surface waxes, cell wall components, and other leaf surface features to optimize their role in the climates where the bryophytes live.

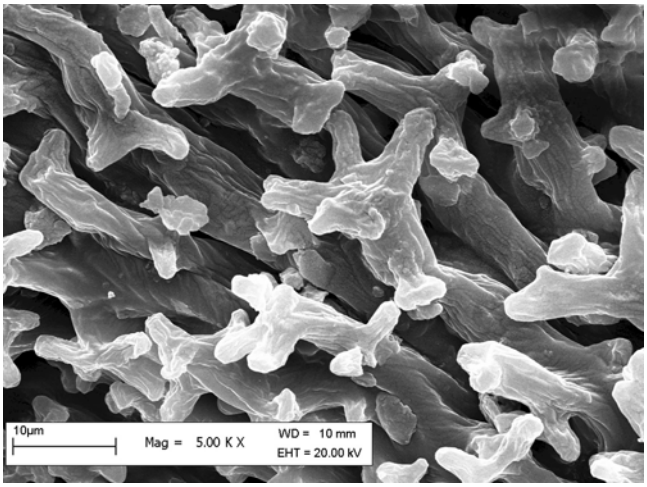

Figure 140. ***Syntrichia caninervis*** SEM of papillae on abaxial leaf surface. Photo by Zhang Yuan Ming.

Leaf Bases and Alar Cells

Many mosses have the advantage of enlarged, thin-walled cells at the base of the leaf (**alar cells**) (Figure 141-Figure 142). These serve as entry points for water into the leaf and stem, but in many species their enlargement when fully hydrated also forces the leaf away from the stem, exposing greater surface area for photosynthesis, and perhaps even for water capture.

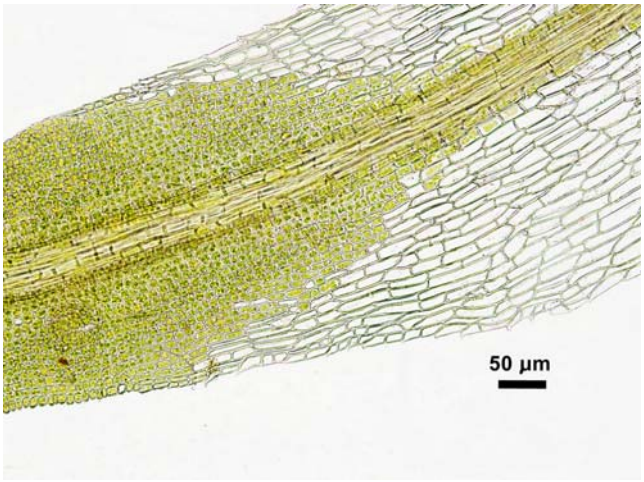

Figure 141. ***Tortella tortuosa*** leaf base showing enlarged hyaline cells where water can enter and cells can swell. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Those alar cells that are thin-walled shrink upon drying and readily gain water as it moves along external capillary spaces. Tucker and coworkers (1975) describe shrinkage of the basal cell cytoplasm during dehydration, creating gas pockets. Upon rehydration, the pockets of gas shrink and disappear within 10-30 seconds and the cytoplasm expands to fill the entire cell. This can explain the rapid unfolding of leaves upon rewetting in many taxa of bryophytes, with alar cells acting like the bulliform (expansion) cells of grasses.

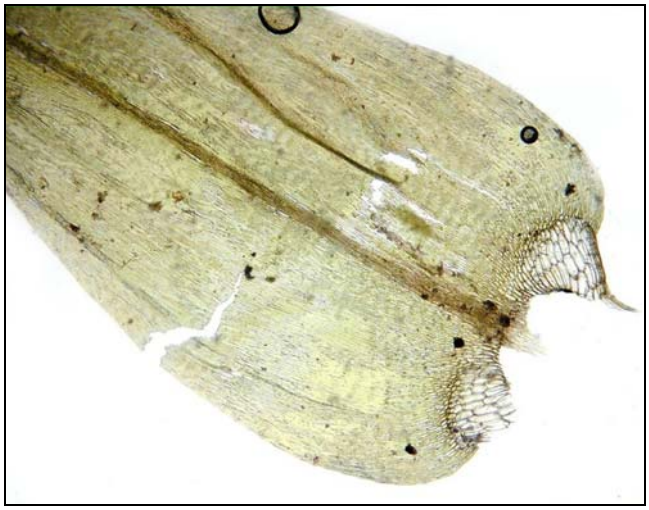

Figure 142. Leaf of ***Calliergon giganteum*** showing costa and enlarged **alar cells** at leaf base. Photo by Michael Lüth, with permission.

Wu *et al*. (2014) demonstrated the importance of adjusting the leaf angle in the desert moss ***Syntrichia caninervis*** (Figure 115, Figure 144). Although this moss is extremely desiccation tolerant, it must balance the need for water conservation with the need for light for photosynthesis when it is hydrated. This is accomplished by the movement of the leaves in response to moisture changes. As leaves become hydrated, they can move from a steep angle of 69-84° with the horizontal axis (Figure 144) to one of only 30° (Figure 115) within 7 seconds of becoming hydrated, with the first leaves moving within 1 second. They are able to obtain maximum net photosynthetic gain at a shoot relative water content of only 60%. The hyaline cells at the leaf base facilitate the rapid absorption of water, but they also swell and force the leaf away from the stem mechanically. It is interesting that the loss of leaf hair retards the leaf angle adjustment. When water was added to the soil instead of being added as an aerial source of water, the absorption rate was reduced, indicating that most water absorption is through the leaves.

Figure 143. ***Syntrichia caninervis*** leaf showing hyaline cells at the base that force the leaf away from the stem when it is hydrated. Photo by Dorothy Allard.

Figure 144. ***Syntrichia caninervis*** dry showing leaves twisted about the stem. Photo by Misha Ignatov, with permission.

Leaf Cell Shape

Bill Buck once asked me what I thought about the elongate cells in mosses such as ***Fontinalis*** and what the significance of such elongate cells might be, predominant in pleurocarpous mosses but rare in acrocarpous ones. I don't know that either of us has a better answer than we did then, but long, narrow cells should have an advantage in water movement. Elongate cells mean that fewer end walls must be crossed for water and other substances to traverse the interior of the leaf from tip to base or vice versa. The split between acrocarpous and pleurocarpous mosses suggests to me that the innovation of elongate cells, perhaps unnecessary in aquatic ancestors, occurred early in the evolution of pleurocarpous mosses and was rarely achieved among the acrocarpous species.

In the acrocarpous moss ***Bryum pseudotriquetrum***, this elongation is partially achieved (Figure 145). This is a moss of wet habitats that dry out. The leaves are usually out of the water, and having somewhat elongated cells should improve transport.

Figure 145. ***Bryum pseudotriquetrum*** leaf showing somewhat elongate cells, bordered by longer cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that many acrocarpous mosses have short leaf cells and tend to be more endohydric, whereas the pleurocarpous mosses, largely lacking a central strand and endohydric conduction, have mostly elongate leaf cells. Although these elongate cells would seemingly facilitate conduction between cells and from the leaf surface to the stem, we lack experimental evidence to support this.

Porose Cells

Porose cells provide more cause for speculation. These cells, uncommon among bryophytes, would seem to provide linkages to adjoining cells while permitting the cells to have otherwise thick walls. Such porosity is easily seen in ***Dicranum polysetum*** (Figure 146). I am unaware of any experiments to demonstrate that this is actually true or to compare the rate of transport in leaves with such cells to those in leaves with non-porose cell walls.

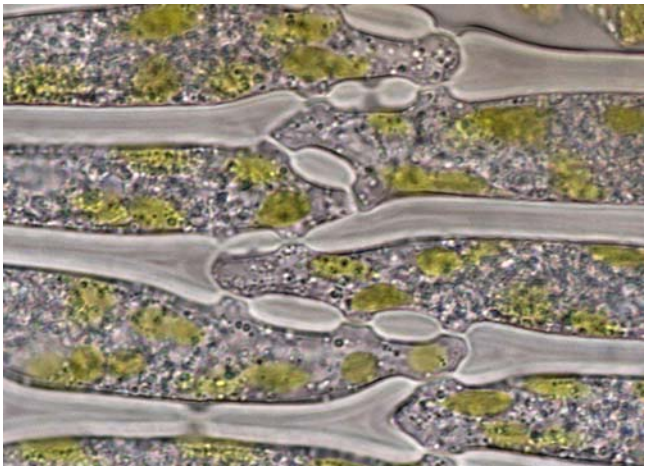

Figure 146. ***Dicranum polysetum*** leaf cell wall structure. Photo by Walter Obermayer, with permission.

Hyalocysts

Colorless or **hyaline** cells (Figure 147) are typical of leaves of ***Sphagnum*** (Figure 148) and ***Hedwigia*** (Figure 134), and the awns of numerous xerophytes. Frahm (1985) examined the correlation between **hyalocysts** and habitat in ***Campylopus*** (Figure 149). ***Campylopus shawii*** occurs in wet swamps where it can obtain and store water easily; it has large ventral hyalocysts. ***Campylopus setifolius***, on the other hand, grows on wet, dripping rocks that dry out occasionally; it has smaller hyalocysts, presumably to reduce the water loss to evaporation from these cells. The presence of ventral hyalocysts in ***C. flagelliferus*** (Figure 149) seem to adapt it to its life restricted to the bark of living trees where it needs a means of rapid water uptake.

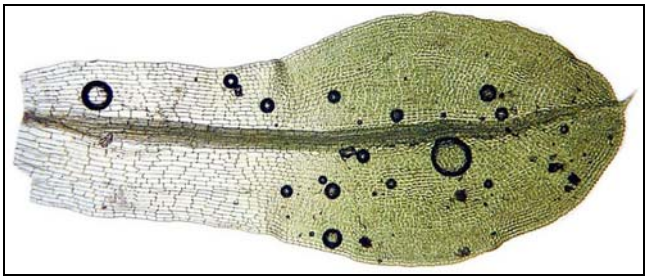

Figure 147. Leaf of ***Tortula vahliana*** showing hyalocysts in basal half of leaf. Photo by Michael Lüth, with permission.

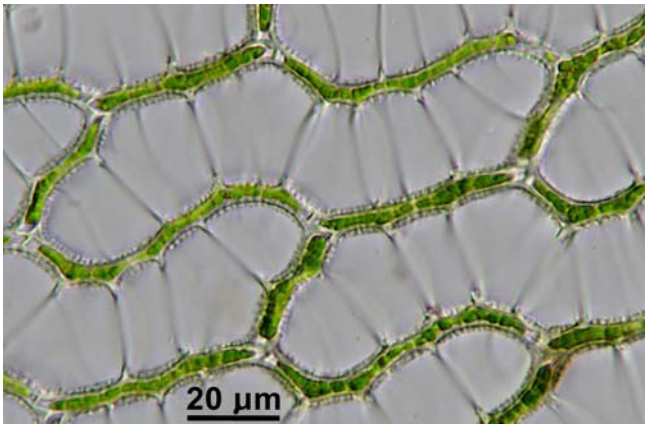

Figure 148. ***Sphagnum papillosum*** leaf cells showing large hyaline cells with fibrils and green photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 149. ***Campylopus flagelliferus***, an epiphyte with ventral hyalocysts. Photo by Jan-Peter Frahm, with permission.

Species of the cushion moss, ***Leucobryum*** (Figure 18, Figure 150), appear very succulent because of the hyalocysts among the photosynthetic cells. In this case, the leaf is several cells thick and the hyalocysts give them a whitish appearance. ***Leucophanes*** (Figure 151-Figure 152) has two different types of hyalocysts. The base of the leaf has a V-shaped arrangement of hyaline cells and the leaf lamina has an upper and lower layer of hyaline cells surrounding the photosynthetic cells.

Figure 150. ***Leucobryum juniperoideum***, showing the thick, whitish leaves. Photo by Michael Lüth, with permission.

Figure 151. ***Leucophanes molleri*** leaf showing v-shaped hyaline base. Photo courtesy of Noris Salazar Allen.

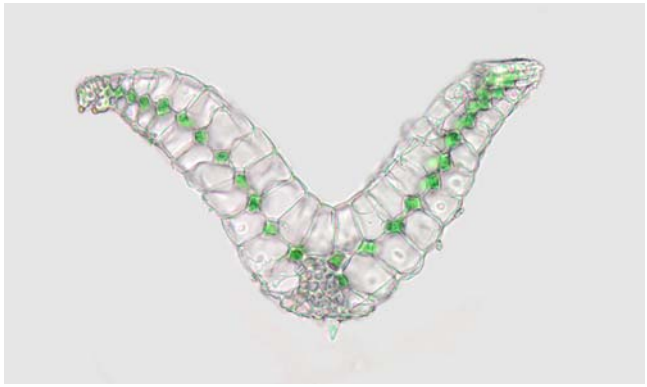

Figure 152. Cross section of ***Leucophanes molleri*** leaf showing hyaline cells surrounding the photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Sphagnum species are considered xerophytic hydrophytes with many adaptations to deal with periodic drought (Andrus 1986). Living in a watery mire for most of the year, this genus has no internal conducting system and must face a severe threat of drying in the full sun of the summer when the water table is low. The ectohydric ***Sphagnum*** is a poor drought tolerator, but a relatively good drought avoider (Li *et al.* 1992). It has two types of leaf cells, small photosynthetic cells and large hyaline cells (Figure 153).

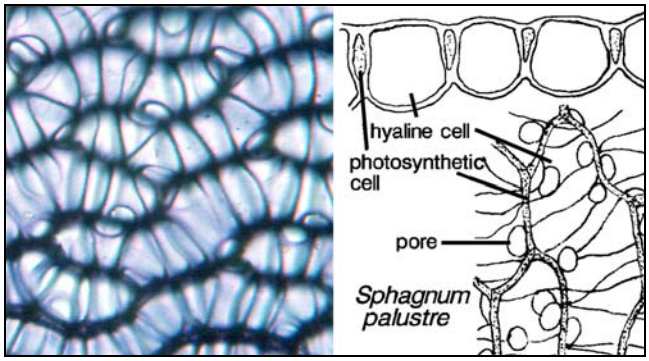

Figure 153. ***Sphagnum*** leaf cell types and pores. **Left:** ***Sphagnum*** leaf cells stained with crystal violet. Photo by Janice . Glime. **Right:** ***Sphagnum palustre*** photosynthetic and hyaline cells as seen in cross section (**upper**) and flat (**lower**). Drawings by Margaret Minahan.

Hyaline cells bathe the photosynthetic cells in water by providing a reservoir. Since the hyaline cell is a dead cell, its sole purpose seems to be to supply water to the photosynthetic portion of the leaf. These cells give some species of ***Sphagnum*** (Figure 153-Figure 154) the ability to hold up to 25 times their own mass in water (Andrus 1986).

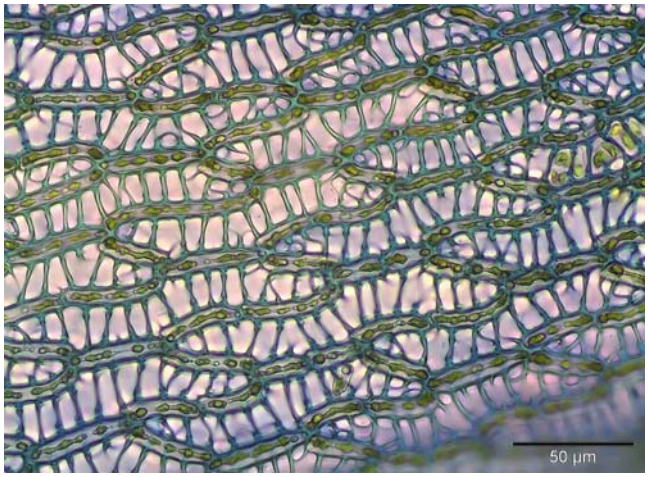

Figure 154. ***Sphagnum fallax*** leaf cells under normal nutrient conditions. Hyaline cells disappear under certain high N or low carbohydrate conditions in culture. Photo by Kristian Peters, with permission.

Transplant studies indicate that species of ***Sphagnum*** differ in abilities to inhabit different heights above the water level, and these differences seem to correlate with the positions they occupy in the field (See Li *et al.* 1992, Rydin 1993, and discussion in competition chapter). Studies by Hintikka (1972) hint that the mechanism for some of these adaptive differences may not relate to water, but to other factors associated with submersion. When grown in sterile culture, ***S. fallax*** (Figure 154) produced no hyaline cells in the presence of high ammonium, high organic nitrogen, or low carbohydrates. In nature, ammonia from decomposing plant matter would be greater under water than around emergent plants, quickly diffusing away in the atmosphere. Likewise, amino acids from organic decomposition would be present only in submersion water, not in rainfall. Response to low carbohydrates may be a limit in carbon available for making additional cell wall tissue, a need for an energy source, or it could relate to CO_2 from decomposing plant material in interstitial bog or fen waters.

Sphagnum seems to require a tremendous water content to achieve its maximal net photosynthesis, probably supplied by the large reservoir of water in its non-photosynthetic hyaline cells. In ***S. fuscum*** (Figure 155), a hummock top species, 600-1000% saturation was optimal, whereas in ***S. angustifolium*** (Figure 156), which tends to occur somewhat closer to the water surface, 900-1300% was optimal (Silvola & Aaltonen 1984), indicating the greater need for water in species that live closer to the water level. The photosynthetic decrease with water reduction was steeper for ***S. fuscum***, and plants in the field generally occurred where their water content was within this 600-1000% range. In ***S. angustifolium***, however, plants often occurred where their water content was outside their optimum range, thus defining narrow and broad relative niches.

Sphagnum is well known for its morphological plasticity in response to water availability (Miller 1991). For example, ***Sphagnum magellanicum*** (Figure 157) and ***S. papillosum*** (Figure 158) in dry conditions produce leaves that are longer (Figure 159) with more pores per cell (Figure 160). Li and coworkers (1992) suggest that these modifications may promote water-holding and absorbing properties.

Figure 155. ***Sphagnum fuscum*** in its typical position atop a hummock. Photo by Michael Lüth, with permission.

Figure 156. ***Sphagnum angustifolium***, a species that lives low on a hummock. Photo by Michael Lüth, with permission.

Figure 157. ***Sphagnum magellanicum***, a species that makes longer leaves under dry conditions. Photo by Janice Glime.

Figure 158. ***Sphagnum papillosum***, a species that makes longer leaves under dry conditions. Photo by Michael Lüth, with permission.

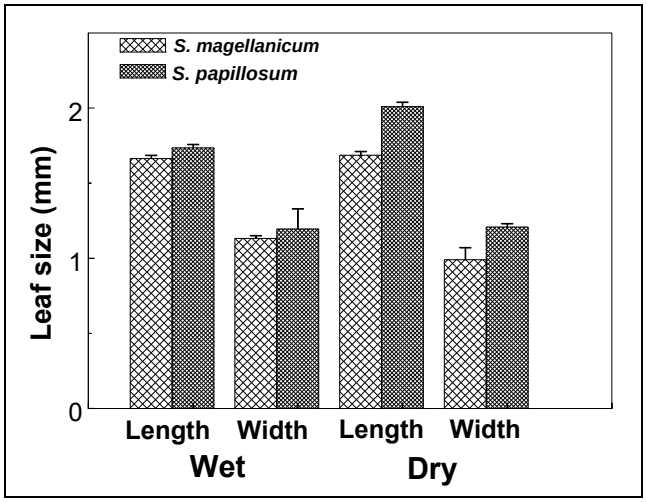

Figure 159. Comparison of leaf dimensions in ***Sphagnum magellanicum***, a drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al*. (1992).

Yet, these two species also differ in their water relations (Li *et al*. 1992). ***Sphagnum magellanicum*** (Figure 157) seems to be a better competitor for water than is ***S. papillosum*** (Figure 158) under dry conditions. This is exhibited by its better water transport ability and greater water content under the same atmospheric moisture conditions (Figure 161). This greater ability may be facilitated by its greater stem diameter due to larger hyaline cells, greater pore number, and smaller leaf size. On the other hand, ***S. papillosum*** (Figure 158) seems to be a better drought tolerator, having a higher survivorship following severe drought conditions.

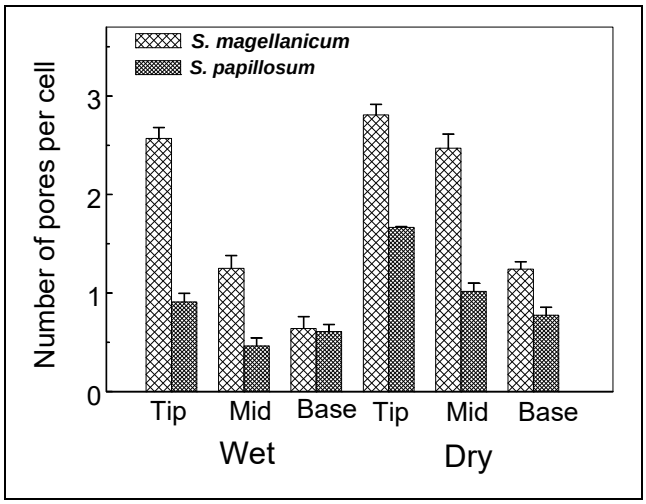

Figure 160. Comparison of number of pores per leaf cell in ***Sphagnum magellanicum***, a more drought-resistant species, and ***S. papillosum***, a more drought-tolerant species. Based on Li *et al*. 1992.

Superiority in water transport permits ***S. magellanicum*** (Figure 157) to occupy a higher position in the hummock than does ***S. papillosum*** (Figure 158). Li and coworkers (1992) found that when the two species grow intermixed in the higher hummock positions, both species grow better than if either is alone, provided at least half the plants are ***S. magellanicum***. They suggest that lateral transport among stems may occur to facilitate this, with ***S. magellanicum*** providing water for both species. If ***S. papillosum*** is dominant, even at somewhat lower positions in the hummock, both dry out more quickly.

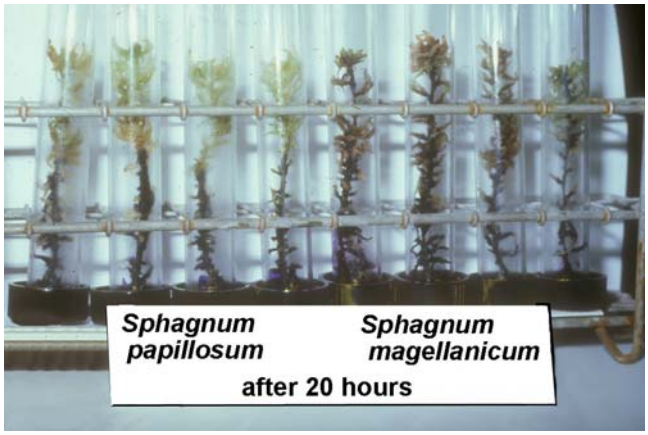

Figure 161. Comparison of distance a water-soluble dye has moved in 20 hours in ***Sphagnum papillosum*** and ***Sphagnum magellanicum***. Photo courtesy of Yenhung Li.

Cancellinae

The **cancellinae** (sing. cancellina) occur in few bryophytes, but especially in the **Calymperaceae**, **Pottiaceae**, ***Encalypta*** (Figure 163-Figure 164), and some species of ***Leptodontium*** (Figure 162). They are large, empty basal leaf cells, usually hyaline, that form a lattice. In the **Calymperaceae**, these are porate (having pores), and may serve as water storage cells.

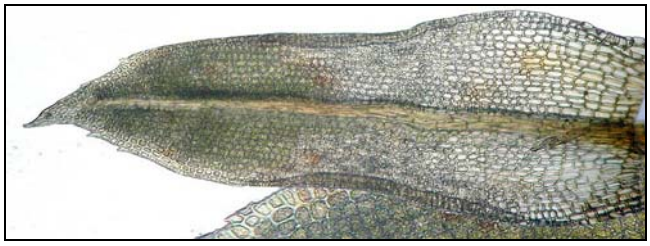

Figure 162. ***Leptodontium*** from the Neotropics showing cancellinae in the upper leaf. Photo by Michael Lüth, with permission.

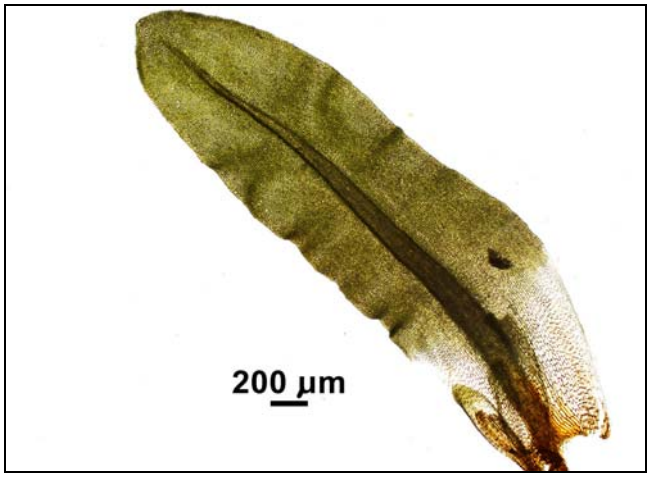

Figure 163. ***Encalypta vulgaris*** leaf showing lattice of cancellinae (gold walls) at base of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

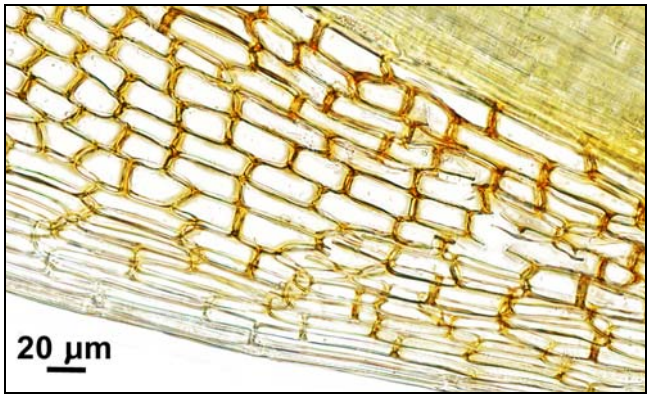

Figure 164. ***Encalypta vulgaris*** leaf showing lattice of cancellinae (cells with gold walls). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Cell Structure

Cells structures can differ in a variety of ways that can affect water uptake, movement, and conservation. These differences include cell wall thickness, cell wall components, pores in the walls, internal papillae, presence of oil bodies, and vacuole size. These differences have the potential to alter the water relations of the leaves.

Cell Walls

Guerra *et al.* (1992) included **incrassate** cell walls among the adaptations of xerophytic mosses. Examples of these include ***Aloina aloides*** (Figure 165-Figure 166) and ***Didymodon fallax***. (Figure 167-Figure 168).

Figure 165. ***Aloina aloides***, a dry habitat moss with incrassate leaf cell walls. Photo by Michael Lüth, with permission.

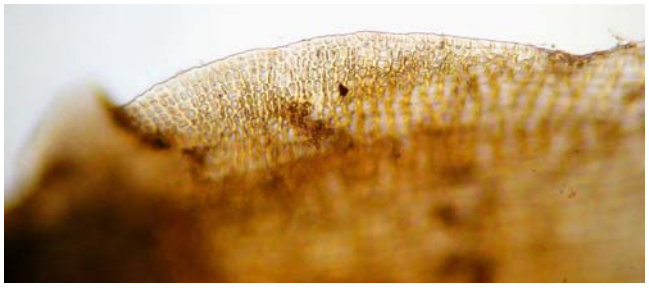

Figure 166. ***Aloina aloides*** leaf cells showing incrassate cell walls. Photo by Heike Hofmann © swissbryophytes <www.swissbryophytes.ch>, with permission.

Figure 167. ***Didymodon fallax***, a dry habitat species. Photo by David T. Holyoak, with permission.

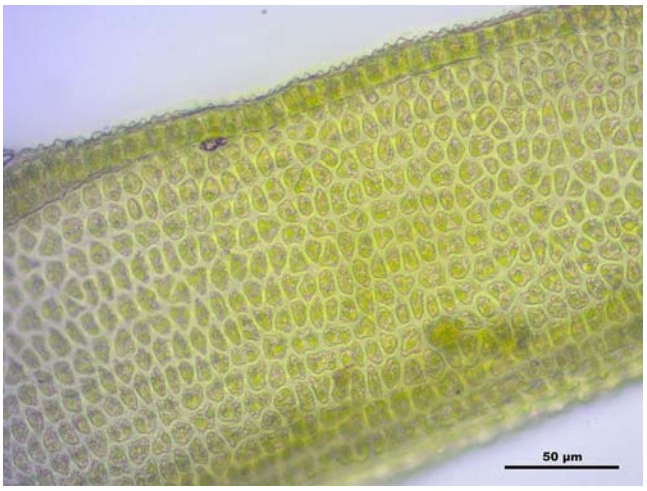

Figure 168. ***Didymodon fallax*** with incrassate leaf cell walls. Photo by Hermann Schachner, through Creative Commons.

Proctor (1979a) contends that coarse leaf cell walls (Figure 169) seem to aid water movement, possibly creating more internal capillary spaces among the fibrils of the cell wall (Proctor 1982). Proctor (1984) noted that mosses of dry habitats tend to have thick cell walls that can occupy more than half the cross section of the leaf. Fajuke (2010) further found that six mosses from Nigeria had thick cell walls that helped them survive desiccation.

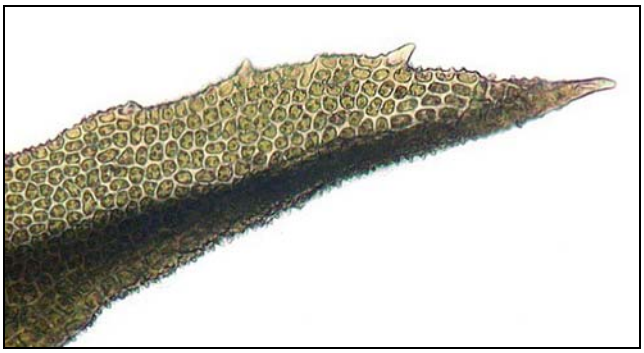

Figure 169. Leaf of ***Zygodon dentatus*** showing thick cell walls and papillae. Photo by Michael Lüth, with permission.

On the other hand, Frey and Kürschner (1991) could find no correlation between thickened cell walls and increasing aridity. Proctor (1982) also pointed out that such xerophytic mosses as ***Syntrichia*** (Figure 170-Figure 171), ***Encalypta*** (Figure 172-Figure 173), and ***Anomodon viticulosus*** (Figure 174-Figure 175) have quite thin walls and external conduction, suggesting that the thick walls are associated with species having internal conduction.

Figure 170. ***Syntrichia ruralis***, a moss of xeric habitats. Photo by Michael Lüth, with permission.

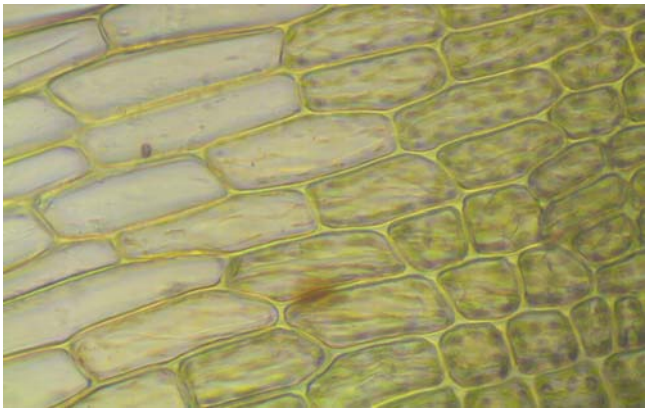

Figure 171. ***Syntrichia ruralis*** leaf lamina cells showing thin walls. Photo by Kristian Peters, with permission.

Figure 172. ***Encalypta rhabdocarpa*** showing xeric habitat in Europe. Photo by Michael Lüth, with permission.

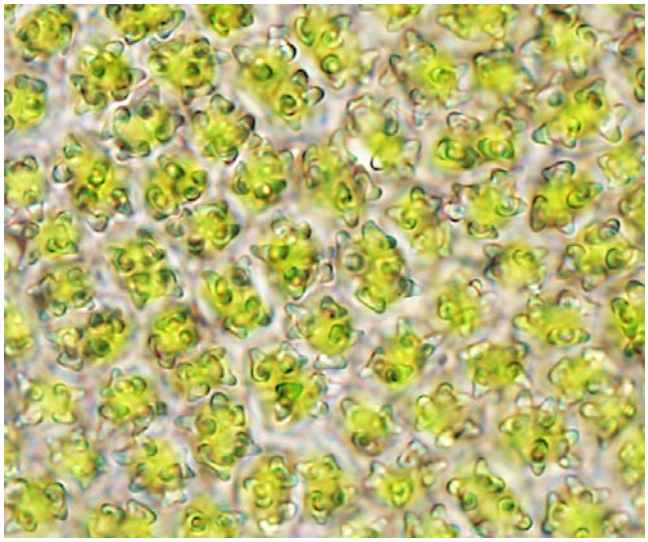

Figure 173. ***Encalypta vulgaris*** leaf cells with branched papillae and thin cell walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 174. ***Anomodon viticulosus***, a xerophytic moss with thin cell walls and papillae. Photo by Janice Glime.

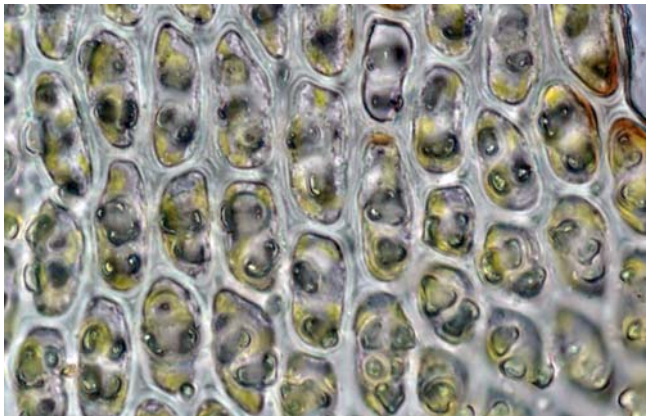

Figure 175. ***Anomodon viticulosus*** leaf cells and papillae. Proctor (1982) considered this species to have thin cell walls, but that does not appear to be the case in this example. Photo by Walter Obermayer, with permission.

The moss ***Rhacocarpus purpurascens*** (Figure 136) appears to have a unique means of facilitating rapid absorption of fog, dew, and rain (Barthlott & Schultze-Motel 1981; Edelmann *et al*. 1998). It has four layers of cell wall with a "peculiar architecture," forming cavities within the wall.

Flexibility of the cell wall is undoubtedly an aid to cell survival. This permits the cells to shrink upon dehydration, up to 50-70% in ***Syntrichia ruralis*** (Figure 176), without allowing for air to enter the drying cells (Moore *et al*. 1982).

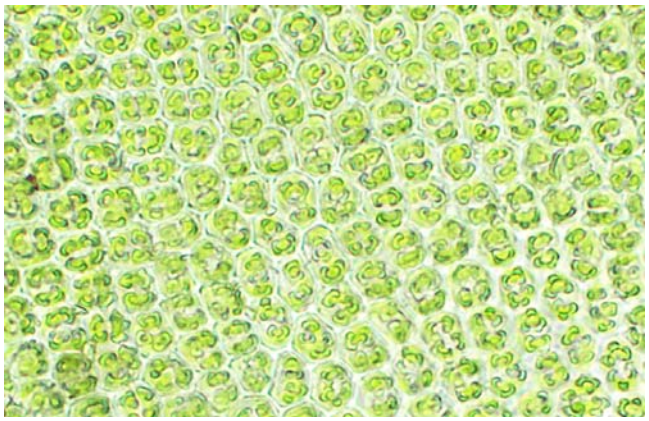

Figure 176. ***Syntrichia ruralis*** leaf cells with c-shaped papillae and thin walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Popper and Fry (2003) suggest that the addition of **xyloglucans** to the cell wall components may have been an important contribution to the ability of bryophytes to invade land. The presence of high concentrations of uronic acids would have permitted these plants to hold nutrient ions until such time as water was available for transport.

Cell walls seem like the first line of defense against desiccation. Autofluorescing compounds that can strengthen these walls are present in sporangial epidermis, spiral thickenings of elaters, and rhizoids, and leaf cells in the special case of ***Sphagnum*** (Figure 177) Kroken *et al*. (1996). In charophytes, these resistant compounds have multiple functions that include desiccation resistance and microbial resistance in lower charophytes, a role in embryogenesis in ***Coleochaete*** (Figure 178) and embryophytes, and decay resistance in structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.

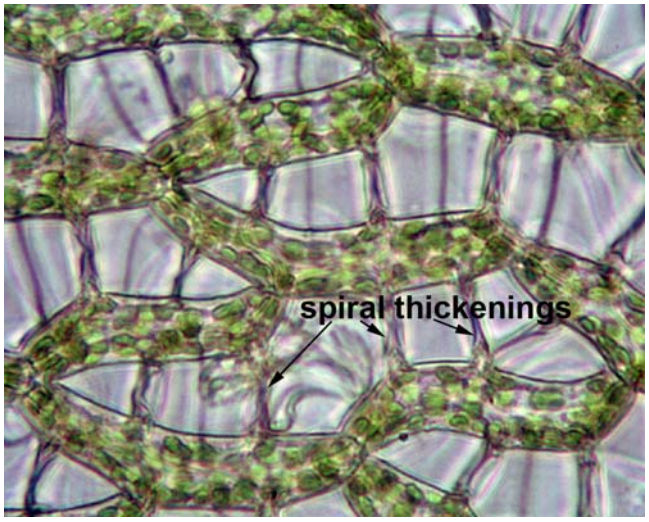

Figure 177. ***Sphagnum palustre*** cells showing the spiral thickenings on the hyaline cells. Photo by Malcolm Storey, through Creative Commons.

Figure 178. ***Coleochaete***, an alga with slime papillae and other characters that are more common among bryophytes. Photo by Yuuji Tsukii <http://protist.i.hosei.ac.jp/>, with permission.

It appears that the resistance of cell walls to desiccation is an ancient trait, already present in the green alga ***Coleochaete*** (Figure 178) (Kroken *et al*. 1996). In fact, it seems to be unique to ***Coleochaete*** among the charophytes and the resistance is produced in response to desiccation stress.

But bryophytes also have this ability – sexual reproduction induces autofluorescence in the cell walls of well-hydrated tissues at the placental junction, suggesting that these cell walls are endowed with compounds (phenols?) that endow them with desiccation resistance (Kroken *et al*. 1996). A similar phenomenon occurs in the gametophyte tissue at the apical end of the **pseudopodium** (gametophyte stalk that suspends the ***Sphagnum*** capsule away from the plant; Figure 179), suggesting a similar role to that of other bryophytes and even ***Coleochaete*** (Figure 178).

Figure 179. ***Sphagnum*** **pseudopodia** supporting capsules. The swollen upper end is desiccation tolerant and houses the foot of the sporophyte. Photo by Joan Edwards, with permission.

Lignin: The presence of lignin in bryophytes has been a controversial topic for ages. Lignins are present in xylem and sclerenchyma cells of tracheophytes. To demonstrate whether these substances might be present in bryophyte and charophyte cell walls, Ligrone *et al*. (2008) examined the charophyte *Nitella* and a number of bryophytes. Using polyclonal antibodies that labelled lignified walls in tracheophytes, they found that these also bound to the cell walls of bryophytes. But rather than the specific locations found in tracheophytes, the locations in mosses and liverworts were not tissue-specific. Hornworts (***Megaceros flagellaris*** and ***M. fuegiensis***; Figure 180) differed somewhat in that labelling was stronger in pseudoelaters and spores than in other cell types. Cell walls were likewise labelled in the charophyte *Nitella*, but a lack of binding suggested that lignins or lignin-like substances were absent in *Coleochaete*.

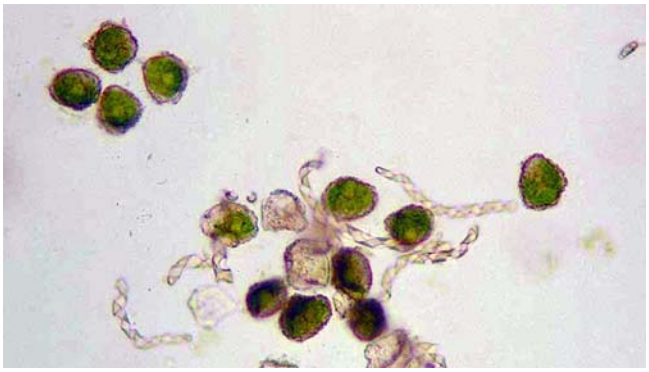

Figure 180. ***Megaceros*** spores and elaters, a genus in which lignin labelling is stronger in spores and elaters than in other cell types. Photo by Christine Cargill, with permission.

Oil Bodies

Oil bodies are common in the leaf cells of leafy liverworts (Pfeffer 1874; Garjeanne 1903; Müller 1905, 1939; Schuster & Hattori 1954; Pihakaski 1972a, b; Stewart 1978; Schuster 1992; Asakawa 2004), but similar structures are generally absent in mosses. Kronestedt (1983) found that they had seasonal variability in the nature of the matrix and the amount of lipophilic material in the floating liverwort ***Ricciocarpos natans*** (Figure 181). The globules can coalesce to form larger units. Their role has remained a mystery (He *et al*. 2013), but recently several researchers have provided evidence that they may have a crucial role in desiccation tolerance.

Oil bodies seem to have different developmental pathways in different species. Pihakaski (1966, 1968, 1972a) compared their development in two leafy liverworts – ***Bazzania trilobata*** (Figure 182-Figure 183) and ***Lophozia ventricosa*** (see Figure 184). The component parts are the same in both species: an outer membrane that envelops the whole oil body, a granular stroma layer that varies in size and thickness, specific globules enveloped by the stroma layer, and a thin inner membrane that surrounds the specific globules. But the oil bodies in these two species develop in different ways. In ***B. trilobata***, they develop from vacuole-like formations in the shoot apex or in leaf primordia where certain substances segregate. In this species, granular dense bodies are visible in the cells of the shoot apex, but these shrink in size as oil bodies develop and are absent in the mature leaf cells. In ***L. ventricosa*** they originate by aggregation and fusion of lipid bodies.

Figure 181. ***Ricciocarpos natans***. Photo by Štěpán Koval, with permission.

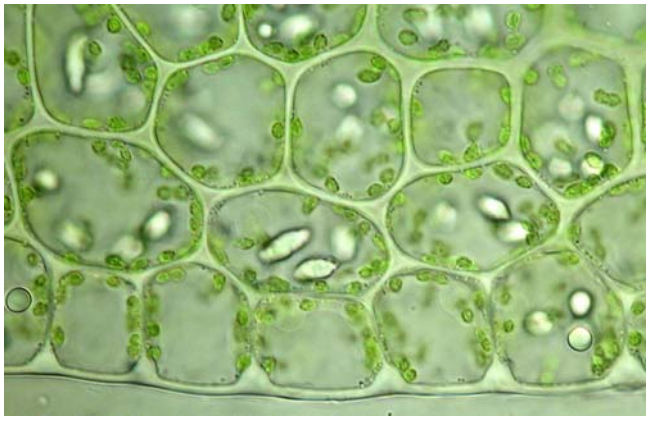

Figure 182. Oil bodies (transparent) in leaf cells of ***Bazzania trilobata***. Photo by Walter Obermayer, with permission.

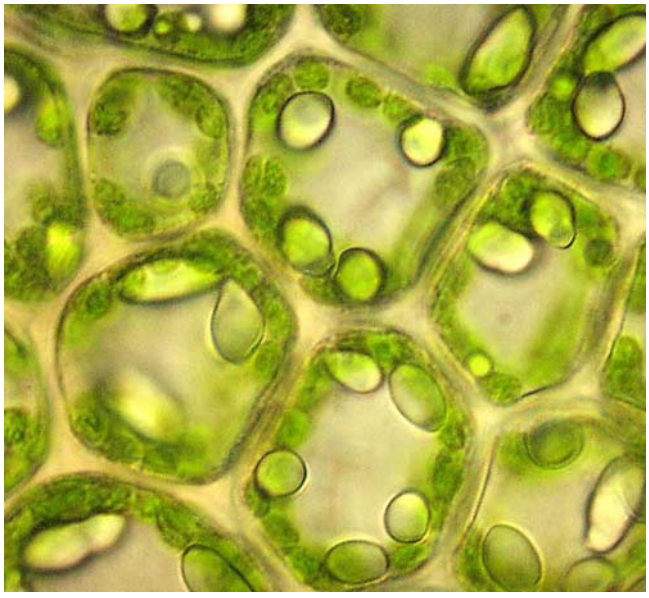

Figure 183. Oil bodies (transparent) in leaf cells of ***Bazzania trilobata***. Photo by Walter Obermayer, with permission.

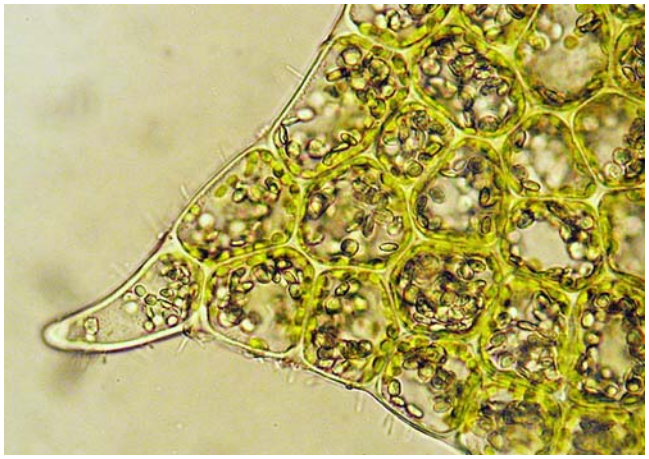

Figure 184. ***Lophozia incisa*** leaf cells with oil bodies. Photo by Walter Obermayer, with permission.

Duckett and Ligrone (1995) followed the development of oil bodies in gemmae of ***Odontoschisma denudatum*** (Figure 185). They appear suddenly early in development, forming flat structures associated with the endoplasmic reticulum. Suire (2000) provided evidence that liverwort oil bodies are secretory cell compartments that originate from the endoplasmic reticulum. The oil bodies remain closely associated with the cytoplasmic lipid bodies throughout development but do not fuse with them. Finally they take on their ultimate shape and become suspended by fine cytoplasmic bridges within the vacuoles.

Oil bodies are notorious for disappearing in herbarium specimens. Pressel *et al*. (2009) described this behavior for desiccation-tolerant liverworts. They found that while they are dry, they remain substantially unchanged, but when they are rewet, they initially change drastically, becoming flattened. It requires up to 48 hours for them to regain their normal shapes. However, if the liverworts are dried faster than would typically happen in nature, they, and other organelles, disintegrate when the liverwort is rewet. Pressel *et al*. suggested that loss of shape upon normal rewetting could be evidence of a shift in soluble carbohydrates or other substances into the cytosol, indicating that the oil bodies may be critical to the desiccation tolerance of liverworts.

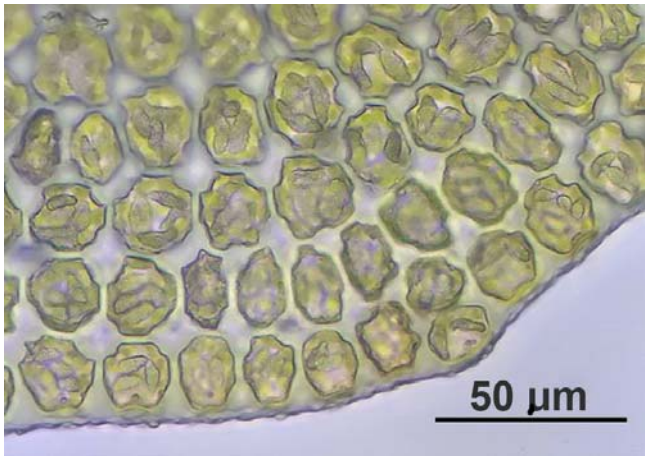

Figure 185. ***Odontoschisma denudatum*** "cuticular" papillae (see leaf edge), leaf cells, and oil bodies. Photo by Kristian Peters, with permission.

Galatis *et al*. (1978) found phenolic and "polysaccharidic" compounds but no protein in the oil bodies of ***Marchantia palacea*** (Figure 186). On the other hand, He *et al*. (2013) reported that in ***Marchantia polymorpha*** (Figure 187) the oil bodies (Figure 188) contain a protein complex that is immunologically related to plastid and cytoplasm enzymes of the **isoprenoid** synthesis (isoprenoids belong to a class of organic compounds composed of two or more units of hydrocarbons, with each unit consisting of five carbon atoms in a specific pattern; they have a wide range of roles in physiological processes of plants and animals). Suire *et al*. (2000) similarly found isoprenoid biosynthetic enzymes similar to those found in plastids and the cytosol of ***Marchantia polymorpha***. The suggested paucity of protein in the oil droplets of liverworts (Galatis *et al*. 1978) is likewise in sharp contrast with that found in the green alga ***Chlamydomonas reinhardtii*** (Moellering & Benning 2010). In this alga, 259 proteins were associated with lipid droplets.

Figure 186. ***Marchantia paleacea*** thallus with archegoniophores, a species with phenolic and "polysaccharidic" compounds but no protein in the oil bodies. Photo from Briofitas de Mexico, through Creative Commons.

Figure 187. ***Marchantia polymorpha*** with ice crystals. This species has oil bodies that contain a protein complex. Photo by David Taylor, with permission.

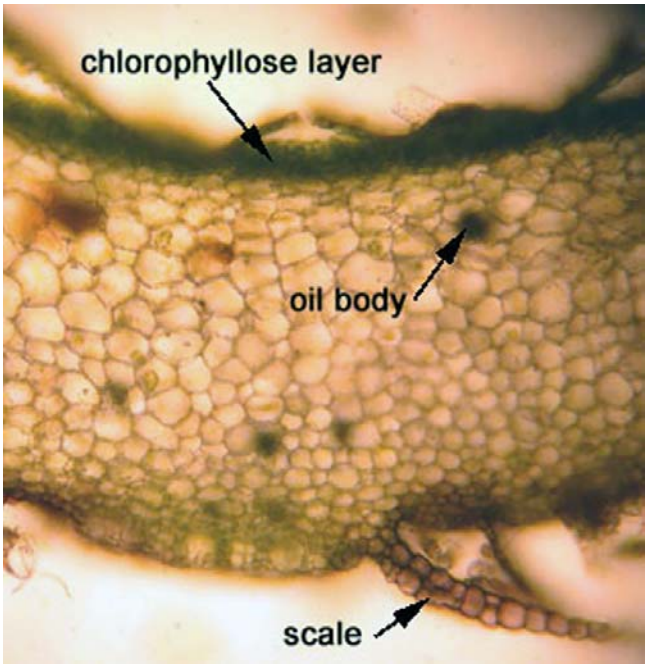

Figure 188. ***Marchantia polymorpha*** thallus vertical section showing oil bodies. Photo from Botany Department, University of British Columbia, with permission.

Oil bodies of liverworts produce mono-, sesqui-, and diterpenoids, aromatic compounds such as bibenzyl, bis-bibenzyls, and acetogenins (Asakawa 2008; Asakawa *et al*. 2013). These often aromatic compounds have such activities as causing allergenic contact dermatitis, antimicrobial action, antifungal and antiviral action, cytotoxicity, insecticidal action, insect antifeedant, superoxide anion radical release, 5-lipoxygenase, calmodulin, hyaluronidase, cyclooxygenase, DNA polymerase β, and α-glucosidase and NO production inhibition, antioxidant, piscicidal, neurotrophic, and muscle relaxation. But these are mostly uses of interest to humans and do little to tell us how the liverwort benefits from them.

It appears that mosses do have their own version of oil bodies. Huang *et al*. (2009) reported abundant oil bodies in the photosynthetic gametophyte and the spores of ***Physcomitrella patens*** (Figure 189-Figure 190). These researchers found that neutral lipids in these oil bodies in the gametophyte were largely steryl esters and triacylglycerols, and unlike some reports on the liverwort oil bodies, they had proteins. These proteins were programmed by three oleosin genes. The expression of these oleosin genes were tissue specific. Structural proteins cover the surfaces of the lipid droplets and prevent them from coalescing during desiccation (Huang *et al*. 2009; He *et al*. 2013).

The number of oil bodies in apical gametophyte tissue decreases during the production of sex organs in ***Physcomitrella patens*** (Figure 189-Figure 190) (Huang *et al*. 2009). In spores, the oil bodies serve as food reserves for **gluconeogenesis** (formation of glucose from smaller molecules) and are equivalent to those of seed oil bodies. It appears that these oil bodies have an energy function for reproduction, but could they be important in providing the energy needed during rehydration as well?

Figure 189. ***Physcomitrella patens***, a species produces abundant oil bodies in its leafy gametophyte and spores, but the oil bodies decrease during sex organ production. Photo by Michael Lüth, with permission.

Figure 190. ***Physcomitrella patens*** sporophyte with spores that contain oil bodies. Photo by Ralf Reski Lab through Wikipedia Commons, with permission.

Vacuoles

Bryophytes, for some reason, were long thought to lack vacuoles. However, this is not the case, as demonstrated in the liverwort ***Lunularia cruciata*** (Figure 191) (Carginale *et al*. 2004), the mosses ***Physcomitrella patens*** (Figure 189) (Nagao *et al*. 2005), ***Ephemerum cohaerens*** (Figure 192) (Kwok & Rushing 1999), and ***Fontinalis antipyretica*** (Figure 193) (Bruns 1998). In fact, the vacuoles can be quite large, as witnessed by the chloroplasts crowded around the periphery of the cell in many species. But there has been no systematic study to indicate which bryophytes have vacuoles and which do not. We might ask if there is some correlation between the ability to withstand drought or to take up water, or even to hold on to cellular water as the environment dries and the presence of one or more vacuoles.

Vacuoles are known in plants to contain solutes that control the water uptake by the vacuole (Taiz & Zeiger 1991). In bryophytes, Nagao *et al*. (2005) have demonstrated that ABA affected the appearance of vacuoles during treatment with freezing. Since ABA is also involved in drought tolerance and has resulted in the increased osmotic concentration of protonemal cells, this mechanism of vacuolar preparation should be explored for possible relationships to drought tolerance in various

bryophytes. Could presence of a vacuole help the cell take in water more quickly by storing solutes that create an osmotic gradient, yet are safely out of the way of cellular metabolism? Could it also have a role in the ability of the cells to shrink as they dry and expand when wet?

Figure 191. ***Lunularia cruciata*** thallus section through gemmae cup. This is a species of thallose liverwort with demonstrated vacuoles. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 192. ***Ephemerum cohaerens*** leaf, a species with demonstrated cell vacuoles in the leaves. Photo by Dick Haaksma, with permission.

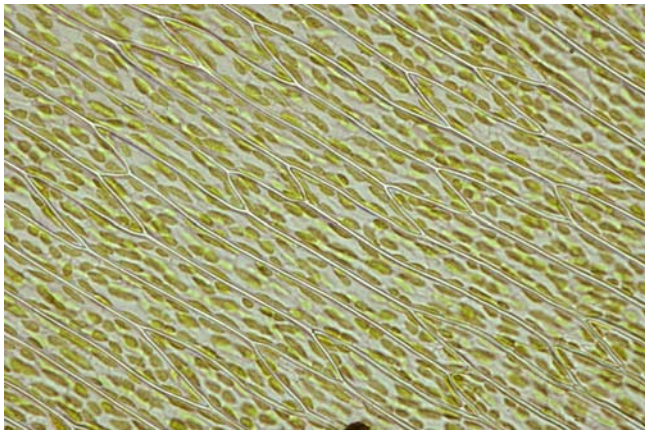

Figure 193. ***Fontinalis antipyretica*** leaf cells, a species with demonstrated cell vacuoles in the leaves. Photo by Janice Glime.

Slime Papillae

In leafy liverworts, **slime papillae** on marginal leaf cells can help to absorb and hold water, as in the leaf margins of ***Porella*** (Figure 194) and ***Heteroscyphus*** (Figure 195) (Daniels 1998). The presence of slime papillae in ***Takakia*** (Figure 196) was among the reasons why several bryologists originally considered that genus to be a liverwort, but capsule structure confirmed its similarity to mosses.

Figure 194. ***Porella pinnata***, a species with slime papillae on the leaf margins. Note white margins at arrows on right. Photo by Des Callaghan, with permission.

Figure 195. ***Heteroscyphus coalitus***, a leafy liverwort with slime papillae. Photo by Tom Thekathyil, with permission.

Figure 196. ***Takakia lepidozioides*** slime papillae. Photo from the Herbarium of Hiroshima University, with permission.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves**, **concave leaves**, **crispate leaves**, **plications**, **revolute** or **involute margins**, **lamellae**, **multi-layered leaves**, **lobules, hair points**, **papillae**, **costae**, **stereids**, **borders**, **leaf teeth**, **teniolae**, **alar cells**, **hyaline cells**, **cancellinae**, **resistant cell walls**, **oil bodies**, and **vacuoles**, aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Overlapping leaves, **concave leaves**, **revolute margins**, and **involute margins** help to hold water in capillary spaces. **Alar cells** provide a point of entry through thin walls that balloon up and mechanically spread the leaves. The **costa** and **border** cells may move water more quickly because the cells are long and have fewer end walls to be crossed. **Plications** permit leaf expansion in hydrated leaves and conserve moisture in drying conditions, as do **twisting** and **contorted** leaves. **Hair points** collect water from fog and dew and slow down drying by reducing exposed surface area of the leaf above. In leafy liverworts, **lobules** retain water for species of dry habitats. **Lamellae** may repel water and prevent water logging in some species, but hold water in capillary spaces in others.

Cell walls may contain **phenols** and other fluorescing materials similar to lignin to resist water loss. **Oil bodies** may provide rehydration energy, but their role in water relations is still poorly understood. **Vacuoles** hold water within the cell and permit expansion and contraction of the cell. **Slime Papillae** may contribute to absorption and holding of water.

Acknowledgments

An earlier version of this chapter benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. Ron Gratz translated part of the work by Loeske. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. I was fortunate to have Ken Kellman ask on Bryonet for examples of bryophytes with a demonstrated cuticle; he was kind enough to share his collected references with me. Thank you to Noris Salazar Allen for sending me the leaf images of *Leucophanes*.

Literature Cited

Andrus, R. E. 1986. Some aspects of *Sphagnum* ecology. Can. J. Bot. 64: 416-426.

Asakawa, Y. 2004. Chemosystematics of the Hepaticae. Phytochemistry 65: 623-669.

Asakawa, Y. 2008. Liverworts - Potential source of medicinal compounds. Current Pharm. Design 14: 3067-3088.

Asakawa, Y., Ludwiczuk, A., and Nagashima, F. 2013. Phytochemical and biological studies of bryophytes. Phytochemistry 91: 52-80.

Baker-Brosh, K. F. and Peet, R. K. 1997. The ecological significance of lobed and toothed leaves in temperate forest trees. Ecology 78: 1250-1255.

Barthlott, W. and Schultze-Motel, W. 1981. Zur Feinstruktur der Blattoberflächen und Systematischen Stellung der Laubmoosgattung *Rhacocarpus* und anderer Hedwigiaceae. Willdenowia 11: 3-11.

Basile, D. V. and Basile, M. R. 1987. Leaf arrangement in relation to external water conduction in leafy liverworts (Jungermanniales). Mem. N. Y. Bot. Gard. 45: 179-185.

Bayfield, N. G. 1973. Notes on water relations of *Polytrichum commune* Hedw. J. Bryol. 7: 607-617.

Bell, G. 1982. Leaf morphology of arid-zone moss species from South Australia. J. Hattori. Bot. Lab. 53: 147-151.

Bowen, E. J. 1933. The mechanism of water conduction in the Musci considered in relation to habitat. III. Mosses growing in dry environments. Ann. Bot. 47: 889-912.

Bruns, I. 1998. Induktion thiolhaltiger Peptide im Wassermoos *Fontinalis antipyretica* L. ex Hedw. unter Schwermetalleinfluß und deren Nutzung als Biomarker für Schwermetallbelastungen aquatischer Systeme. Dissertation zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.) vorgelegt an der Mathematisch-Naturwissenschaftlich-Technischen Fakultät der Martin-Luther-Universität, Halle-Wittenberg.

Carginale, V., Sorbo, S., Capasso, C., Trinchella, F., Cafiero, G., and Basile, A. 2004. Accumulation, localisation, and toxic effects of cadmium in the liverwort *Lunularia cruciata*. Protoplasma 223: 53-61.

Chang, S.C., Lai, I-L., and Wu, J.-T. 2002. Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in northeastern Taiwan. Atmospheric Res. 64: 159-167.

Clee, D. A. 1937. Leaf arrangement in relation to water conduction in the foliose Hepaticae. Ann. Bot. N. S. 1: 325-328.

Cornelissen, J. H. C. and Ter Steege, H. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry forest of Guyana. J. Trop. Ecol. 5: 131-150.

Crandall-Stotler, B. J. and Bozzola, J. J. 1990. Ultrastructural details of leaf papilla development in the moss *Andreaeobryum macrosporum*. Proceedings of the XIIth International Congress for Electron Microscopy, San Francisco Press, Inc., CA, pp. 670-671.

Crandall-Stotler, B. J. and Bozzola, J. J. 1991. Ontogeny, structure and function of leaf cell papillae in the moss *Andreaeobryum macrosporum*. Amer. J. Bot. 78(6, suppl.): 4-5.

Crum, H. 1983. Mosses of the Great Lakes Forest. 3rd ed. University Herbarium, University of Michigan, Ann Arbor, MI, 417 pp.

Daniels, A. E. D. 1998. Ecological adaptations of some bryophytes of the Western Ghats. J. Ecobiol. 10(4): 261-270.

Duckett, J. G. and Ligrone, R. 1995. The formation of catenate foliar gemmae and the origin of oil bodies in the liverwort *Odontoschisma denudatum* (Mart.) Dum. (Jungermanniales): A light and electron microscope study. Ann. Bot. 76: 405-419.

Edelmann, H. G., Neinhuis, C., Jarvis, M., Evans, B., Fischer, E., and Barthlott, W. 1998. Ultrastructure and chemistry of the cell wall of the moss *Rhacocarpus purpurascens*

(Rhacocarpaceae): A puzzling architecture among plants. Planta 206: 315-321.

Fajuke, A. A. 2010. Desiccation stress and the effect of humidity in mosses. Not. Sci. Biol. 2: 40-42.

Frahm, J.-P. 1985. The ecological significance of the costal anatomy in the genus *Campylopus*. Abst. Bot. 9, suppl. 2: 159-169.

Frey, W. and Kürschner, H. 1991. Morphologische und anatomische Anpassungen der Arten in terrestrisschen Bryophytengesellschaften entlang eines ökologischen Gradienten in der Judäischen Wüste. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 112: 529-552.

Galatis, B., Apostolakos, P., and Katsros, C. 1978. Histochemical studies on the oil bodies of *Marchantia paleacea* Bert. Protoplasma. 97: 13-29.

Garjeanne, A. J. M. 1903. Die Ölkörper der Jungermanniales. Flora 92: 457-482.

Gradstein, S. R. 1995. Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). Biodiversity and Conservation of Neotropical Montane Forests. The New York Botanical Gardens, Bronx, NY, pp. 321-334.

Guerra, J., Martínez-Sánchez, J. J., and Ros, R. M. 1992. On the degree of adaptation of the moss flora and vegetation in gypsiferous zones of the south-east Iberian Peninsula. J. Bryol. 17: 133-142.

He, X., Sun, Y., and Zhu, R. L. 2013. The oil bodies of liverworts: Unique and important organelles in land plants. Crit. Rev. Plant Sci. 32: 293-302.

Hébant, C. 1970. A new look at the conducting tissues of mosses (Bryopsida): Their structure, distribution and significance. Phytomorphology 20: 390-410.

Heinrichs, J., Gradstein, S. R., Wilson, R., and Schneider, H. 2005. Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene rbcl. Crypt. Bryol. 26: 131-150.

Herzog, T. 1926. Geographie der Moose. Fischer, Jena.

Hintikka, V. 1972. Variation in gametophyte morphology of *Sphagnum fallax* in aseptic culture. Ann. Bot. Fennici 9: 91-96.

Huang, C. Y., Chung, C. I., Lin, Y. C., Hsing, Y. L. C., and Huang, A. H. C. 2009. Oil bodies and oleosins in *Physcomitrella* possess characteristics representative of early trends in evolution. Plant Physiol. 150: 1192-1203.

Koch, K., Bhushan, B., and Barthlott, W. 2008. Diversity of structure, morphology and wetting of plant surfaces. Soft Matter 4: 1943-1963.

Kou, J., Feng, C., Bai, X. L., and Chen, H. 2014. Morphology and taxonomy of leaf papillae and mammillae in Pottiaceae of China. J. Syst. Evol. 52: 521-532.

Kroken, S. B., Graham, L. E., and Cook, M. E. 1996. Occurrence and evolutionary significance of resistant cell walls in charophytes and bryophytes. Amer. J. Bot. 83: 1241-1254.

Kronestedt, E. 1983. Cytology of oil-body cells in *Ricciocarpus natans*. Nord. J. Bot. 3: 547-558.

Kürschner, H. K. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. Turk. J. Bot. 28: 73-84.

Kwok, L. Y., and Rushing, A. E. 1999. An ultrastructural and developmental study of the sporophyte-gametophyte junction in *Ephemerum cohaerens*. Bryologist 102: 179-195.

Larson, D. W. 1981. Differential wetting in some lichens and mosses - the role of morphology. Bryologist 84: 1-15.

Li, Y., Glime, J. M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. J. Bryol. 17: 59-70.

Ligrone, R., Carafa, A., Duckett, J. G., Renzaglia, K. S., and Ruel, K. 2008. Immunocytochemical detection of lignin-related epitopes in cell walls in bryophytes and the charalean alga *Nitella*. Plant Syst. Evol. 270: 257-272.

Loeske, L. 1926. Der Einfluss des Wassers auf Papillen und Mamillen. Folia Cryptog. 1: 215-220.

Loeske, L. 1930. Note about 'Fo. *epilosa*'. Bryologist 33: 22.

Longton, R. E. 1988. Adaptations and strategies of polar bryophytes. J. Linn. Soc. Bot. 98: 253-268.

Lowell, J. 1998. Drought-adaptation in the leaf-border of *Atrichum undulatum*. J. Bryol. 20: 227-230.

Miller, N. G. 1991. Limits of character variation in *Sphagnum trinitense* as expressed by plants growing deeply submerged in a clear water lake. Programme, The Biology of *Sphagnum*, International Association of Bryologists/British Bryological Society, University of Exeter, July 17 & 18 1991.

Moellering, E. R. and Benning, C. 2010. RNA interference silencing of a major lipid droplet protein affects lipid droplet size in *Chlamydomonas reinhardtii*. Eukaryot. Cell 9: 97-106.

Moffett, B. F., Hill, T., and Henderson-Begg, S. K. 2009. Major new sources of biological ice nuclei. The Smithsonian/NASA Astrophysics Data System.

Moore, C. J., Luff, S. E., and Hallam, N. D. 1982. Fine structure and physiology of the desiccation-tolerant mosses, *Barbula torquata* Tayl. and *Triquetrella papillata* (Hook. F. and Wils.) Broth., during desiccation and rehydration. Bot. Gaz. 143: 358-367.

Müller, K. 1905. Beitrag zur Kenntnis der ätherischen Öle bei Lebermoosen. Z. Physiol. Chem. 45: 299-319.

Müller, K. 1939. Untersuchungen über die Ölkörper der Lebermoose. Ber. Dtsch. Bot. Ges. 57: 326-370.

Nagao, M., Minami, A., Arakawa, K., Fujikawa, S., and Takezawa, D. 2005. Rapid degradation of starch in chloroplasts and concomitant accumulation of soluble sugars associated with ABA-induced freezing tolerance in the moss *Physcomitrella patens*. J. Plant Physiol. 162: 169-180.

Obeso, J. R. 1997. The induction of spinescence in European holly leaves by browsing ungulates. Plant Ecol. 129: 149-156.

Pfeffer, W. 1874. Die Ölkörper der Lebermoose. Flora 57: 2-6, 17-27, 33-43.

Pihakaski, K. 1966. An electron microscopy study on the oil bodies of two Hepatic species. Protoplasma 62: 393-399.

Pihakaski, K. 1968. A study of the ultrastructure of the shoot apex and leaf cells in two liverworts, with special reference to the oil bodies. Protoplasma 66: 79-103.

Pihakaski, K. 1972a. Histochemical studies on the oil bodies of the liverworts *Pellia epiphylla* and *Bazzania tribobata*. Ann. Bot. Fenn. 9: 65-76.

Pihakaski, K. 1972b. Studies on the hepatic oil bodies, with special reference to the vacuole-like oil bodies of *Pellia epiphylla*. Univ. Turku Publ. Bot. 170: 1-25.

Popper, Z. A. and Fry, S. C. 2003. Primary cell wall composition of bryophytes and charophytes. Ann. Bot. 91: 1-12.

Pressel, S., Duckett, J. G., Ligrone, R., and Proctor, M. C. F. 2009. Effects of de- and rehydration in desiccation-tolerant

liverworts: A cytological and physiological study. Internat. J. Plant Sci. 170: 182-199.

Pressel, S., P'ng, K. M. Y., and Duckett, J. G. 2010. A cryo-scanning electron microscope study of the water relations of the remarkable cell wall in the moss *Rhacocarpus purpurascens* (Rhacocarpaceae, Bryophyta). Nova Hedwigia 91: 289-299.

Proctor, M. C. F. 1979a. Structure and eco-physiological adaptations in bryophytes. In: Clarke, G. C. S. and Duckett, J. G. (eds.). Bryophyte Systematics, Systematic Association special volume 14, Academic Press, London, pp. 479-509.

Proctor, M. C. F. 1979b. Surface wax on the leaves of some mosses. J. Bryol. 10: 531-538.

Proctor, M. C. F. 1980. Diffusion resistances in bryophytes. In: Ford, E. D., and Grace, J. (eds.). Plants and their Atmospheric Environment. Symp. Brit. Ecol. Soc., pp. 219-229.

Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology, Chapman and Hall, London, pp. 333-381.

Proctor, M. C. F. 1984. Structure and ecological adaptation. In: Dyer, A. F. and Duckett, J. G. (eds.). The Experimental Biology of Bryophytes, Academic Press, London, pp. 9-37.

Proctor, M. C. F. 2004. How long must a desiccation-tolerant moss tolerate desiccation? Some results of two years' data logging on *Grimmia pulvinata*. Physiol. Plant. 122: 21-27.

Proctor, M. C. F., Nagy, Z., Csintalan, Zs., and Takács, Z. 1998. Water-content components in bryophytes: Analysis of pressure-volume relationships. J. Exper. Bot. 49: 1845-1854.

Reese, W. R. 1993. Calymperaceae. Flora Neotropica Monograph 58: 1-101. New York Botanical Garden, USA

Royer, D. L. and Wilf, P. 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. Internat. J. Plant Sci. 167: 11-18.

Royer, D. L., Kooyman, R. M., Little, S. A., and Wilf, P. 2009. Ecology of leaf teeth: A multi-site analysis from an Australian subtropical rainforest. Amer. J. Bot. 96: 738-750.

Rydin, H. 1993. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos 66: 413-423.

Schofield, W. B. 1981. Ecological significance of morphological characters in the moss gametophyte. Bryologist 84: 149-165.

Schuster, R. M. 1992. The oil-bodies of the Hepaticae. I. Introduction. J. Hattori Bot. Lab. 72: 151-164.

Schuster, R. M. and Hattori, S. 1954. The oil-bodies of the Hepaticae. II. The Lejeuneoideae. J. Hattori Bot. Lab. 11: 11-86.

Silvola, J., and Aaltonen, H. 1984. Water content and photosynthesis in the peat mosses *Sphagnum fuscum* and *S. angustifolium*. Ann. Bot. Fennici 21:1-6.

Stewart, G. 1978. Oil bodies of the New Zealand leafy Hepaticae (Jungermanniales). N. Z. J. Bot. 16: 185-205.

Suire, C. 2000. A comparative, transmission-electronic microscopic study on the formation of oil bodies in liverworts. J. Hattori Bot. Lab. 89: 209-232.

Suire, C., Bouvier, F., Backhaus, R. A., B´egu, D., Bonneu, M., and Camara, B. 2000. Cellular localization of isoprenoid biosynthetic enzymes in *Marchantia polymorpha*. Uncovering a new role of oil bodies. Plant Physiol. 124: 971-978.

Taiz, L. and Zeiger, E. 1991. Plant Physiology. Benjamin Cummings Publ. Co., New York, 565 pp.

Tao, Y. and Zhang, Y. M. 2012. Effects of leaf hair points of a desert moss on water retention and dew formation: Implications for desiccation tolerance. J. Plant Res. 125: 351-360.

The Plant List. 2010. Version 1. Accessed 30 October 2013 at <http://www.theplantlist.org>.

Thomas, R. J., Ryder, S. H., Gardner, M. I., Sheetz, J. P., and Nichols, S. D. 1996. Photosynthetic function of leaf lamellae in *Polytrichum commune*. Bryologist 99: 6-11.

Tucker, E. B., Costerton, J. W., and Bewley, J. D. 1975. The ultrastructure of the moss *Tortula ruralis* on recovery from desiccation. Can. J. Bot. 53: 94-101.

Wu, Y., Guo, S.-L., and Fang, F. 2007. Comparison of leaf structures among seventeen moss species collected from different habitats. Acta Botanica Yunnanica 29: 409-417.

Wu, N., Zhang, Y.-M., Downing, A., Aanderud, Z. T., Tao, Y., and Williams, S. 2014. Rapid adjustment of leaf angle explains how the desert moss, *Syntrichia caninervis*, copes with multiple resource limitations during rehydration. Funct. Plant Biol. 41: 168-177.

Zanten, B. O. van. 1975. The hygroscopic movement of the leaves of *Dawsonia* and some other Polytrichaceae. Bull. Soc. Bot. France, Colloque Bryol. 121: 63-66.

Zastrow, E. 1934. Experimentelle Studien aber die Anpassung von Wasser-und Sumpfmoosen. Pflanzenborschung 17: 1-70.

Zhang, J., Zhang, Y.-M., Downing, A., Cheng, J.-H., Zhou, X.-B., and Zhang, B.-C. 2009. The influence of biological soil crusts on dew deposition in Gurbantunggut Desert, Northwestern China. J. Hydrol. 379: 220-228.

Zhang, J., Zhang, Y.-M., Downing, A., Wu, N., and Zhang, B.-C. 2011. Photosynthetic and cytological recovery on remoistening *Syntrichia caninervis* Mitt., a desiccation-tolerant moss from Northwestern China. Photosynthetica 49: 13-20.

Zheng, Y.-P., Xu, M., Zhao, J.-C., Zhang, B.-C., Bei, S.-Q., and Hao, L.-H. 2010. Morphological adaptations to drought and reproductive strategy of the moss *Syntrichia caninervis* in the Gurbantunggut Desert, China. Arid Land Res. Mgmt. 25: 116-127.

CHAPTER 7-4b

WATER RELATIONS: LEAF STRATEGIES – CUTICLES AND WAXES

TABLE OF CONTENTS

Bryophytes Do Have Cuticles 7-4b-2
Sphagnum 7-4b-13
Leafy Liverworts 7-4b-13
Admissibility of Water 7-4b-14
Multiple Forms – Multiple Roles 7-4b-14
Temperature 7-4b-14
Light 7-4b-14
Salt Stress 7-4b-15
Contact Angles and Entry 7-4b-15
Combined Role and Water Relations 7-4b-15
Altitude Protection 7-4b-15
Pollution Protection 7-4b-15
Ozone 7-4b-15
CO_2 ..... 7-4b-15
Repelling Water 7-4b-15
Summary 7-4b-17
Acknowledgments 7-4b-17
Literature Cited 7-4b-17

CHAPTER 7-4b

WATER RELATIONS: LEAF STRATEGIES – CUTICLES AND WAXES

Figure 1. ***Pohlia wahlenbergii*** var. ***glacialis*** in Norway. The drops of water on the surface are being repelled by hydrophobic surface waxes, preventing water logging. Photo by Michael Lüth, with permission.

Bryophytes Do Have Cuticles

Anyone who has observed the speed with which many mosses and leafy liverworts absorb water would assume that they lack waxes. But as we examine these bryophytes with chemical and SEM methods, we find that this assumption is not reliable (Buda *et al*. 2013). For example, the simple moss ***Physcomitrella patens*** (Figure 2) has a cuticle with a chemical composition and structure similar to that of flowering plants. It is likely that the cuticle was a necessary factor in the evolution to land, regulating water status and providing protection from biotic and abiotic stresses. Using knockout genes to create mutant plants that were "severely deficient in cuticular wax accumulation" Buda *et al*. found that these plants also had reduced desiccation tolerance. The gene responsible for the cuticle wax formation in ***Physcomitrella patens*** is the same one as that in *Arabidopsis thaliana*, indicating its evolution early in the invasion of land.

Figure 2. ***Physcomitrella patens***, a moss from which the cuticular wax gene has been isolated. Photo by Janice Glime.

Although thickened waxy cuticles seem to be rare in moss gametophytes, various mosses have some sort of cuticular covering. In some mosses, this is expressed as granules, platelets, or ribbons that are soluble in chloroform (Proctor 1982), satisfying the test for cuticular wax in tracheophytes. This type of cuticle endows ***Pohlia cruda*** (Figure 3), ***P. wahlenbergii*** (=*P. albicans*; Figure 4), ***Saelania glaucescens*** (Figure 55), ***Schistostega pennata*** (Figure 5), ***Pogonatum urnigerum*** (Figure 6), and many **Bartramiaceae** with their **glaucous** (whitish) appearance (Proctor 1982). We shouldn't be surprised that ***Pogonatum urnigerum*** has surface waxes similar to those of tracheophytes, but even primitive mosses such as ***Andreaea rupestris*** (Figure 7) have surface waxes that are similar to the epicuticular waxes of tracheophytes (Haas 1982).

Figure 3. ***Pohlia cruda***, a whitish moss due to cuticular waxes. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 4. ***Pohlia wahlenbergii*** with drops of water, presumably repelled by the surface waxes. Photo by J. C. Schou, with permission.

Figure 5. ***Schistostega pennata*** showing whitish cast of the cuticle. Photo courtesy of Martine Lapointe.

Figure 6. ***Pogonatum urnigerum*** wet, showing the waxy (**glaucous**) appearance of the leaves. Photo by Janice Glime.

Figure 7. ***Andreaea rupestris*** showing slightly glaucous appearance. Photo by Janice Glime.

In addition to most of the species already named, Stránsky *et al*. 1967) found n-alkanes (19-33 carbon atom chains) in ***Leucobryum glaucum*** (Figure 8)**,** ***Rhytidiadelphus triquetrus*** (Figure 9), ***Conocephalum conicum*** (Figure 10), ***Porella platyphylla*** (Figure 11), ***Pellia fabbroniana*** (Figure 12), and ***Pellia epiphylla*** (Figure 13). Even ***Sphagnum*** is known to have waxes (lignoceryl alcohol) in ***S. capillaceum*** (*S. nemoreum*; Figure 59), ***S. fuscum*** (Figure 60), and ***S. magellanicum*** (Figure 61) (Ives & Neill 1958).

Figure 8. ***Leucobryum glaucum*** showing appearance of waxes on a moss with hyaline cells. Photo by Janice Glime.

Figure 9. ***Rhytidiadelphus triquetrus***, a moss expressing waxes that are n-alkanes. Photo by Michael Lüth, with permission.

Figure 10. ***Conocephalum conicum*** showing a waxy surface. Photo by Jan-Peter Frahm, with permission.

Figure 11. ***Porella platyphylla*** on bark, showing slightly glaucous appearance due to wax. Photo by Michael Lüth, with permission.

Figure 12. ***Pellia fabbroniana*** with waxy epidermis and propagules. Photo by Eugenia Ron Alvarez and Tomas Sobota at Plant Actions, with permission.

Figure 13. ***Pellia epiphylla*** showing slightly waxy appearance due to wax on its surface. Photo by Kristian Peters, through Creative Commons.

The documentation of cuticle in bryophyte leaves is somewhat scant. Nevertheless, Proctor (1979b) examined 43 species of mosses and determined that 12 of these have a well developed surface wax on the leaves that is comparable to that of flowering plants. Eight more have traces of wax. Not surprisingly, all of these species are **endohydric** (have internal conduction). If a moss has a waxy or glaucous look, it most likely has surface wax. A good example of this is the leaves of ***Polytrichum*** (Figure 14-Figure 18) On the other hand, ***Atrichum undulatum*** (Figure 19-Figure 21), in the same family (**Polytrichaceae**), has no discernable wax and lacks the waxy appearance. Instead of having leaves that curl inward and wrap around the stem upon drying, members of ***Atrichum*** have wavy leaf surfaces and become contorted when they dry (Figure 22-Figure 23).

Figure 14. ***Polytrichum commune*** leaves showing waxy surface. Photo by James K. Lindsey, with permission.

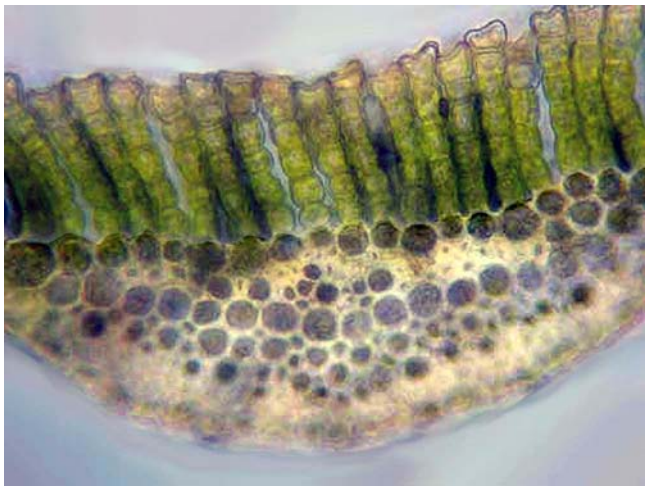

Figure 15. ***Polytrichum commune*** leaf lamellae where waxes are present on the terminal cells. Photo from Botany Department, University of British Columbia, with permission.

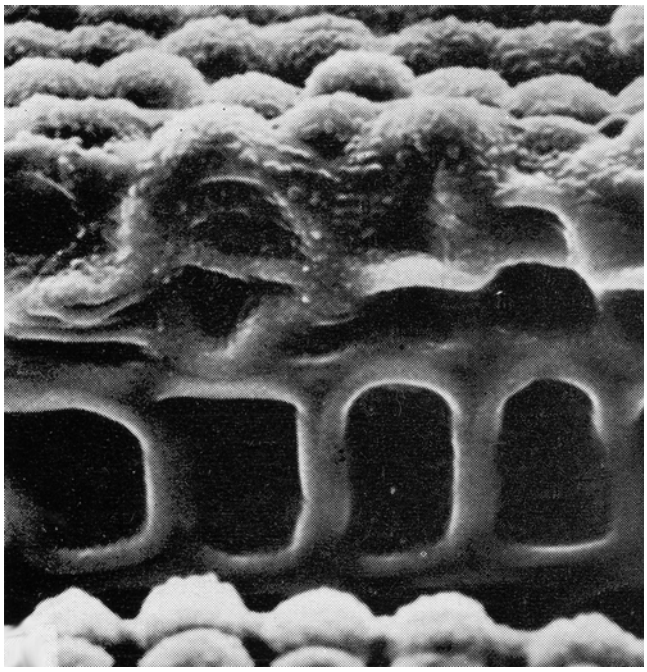

Figure 16. SEM of ***Polytrichum commune*** leaf cuticle. Photo by Michael Proctor, with permission.

Figure 17. ***Polytrichum juniperinum*** showing leaves with lamina rolled over lamellae and waxy appearance. Photo by Michael Lüth, with permission.

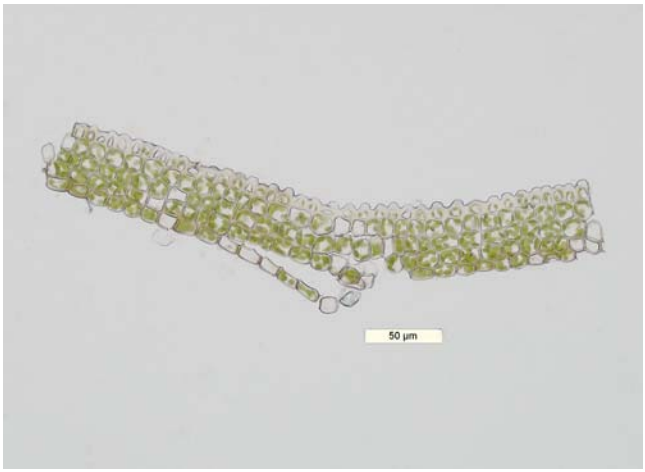

Figure 18. ***Polytrichum juniperinum*** side view of lamella with thick waxy layer on top. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

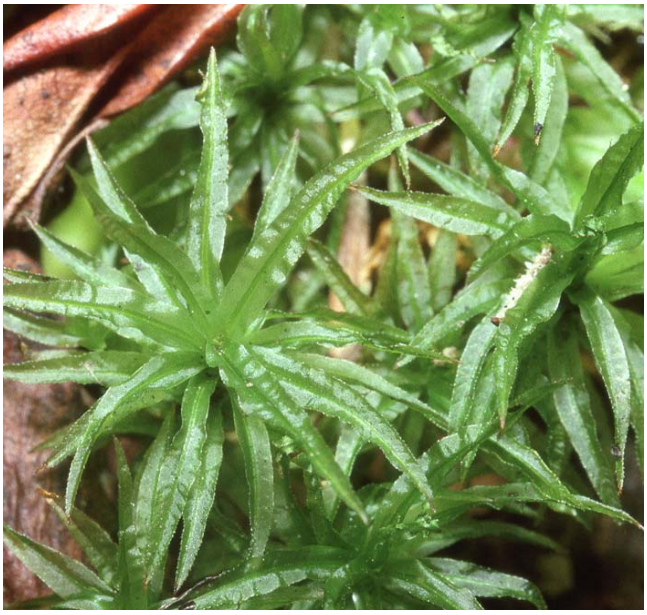

Figure 19. ***Atrichum undulatum*** showing lack of glaucous coloring and presence of wavy leaves that curl and twist when drying. Photo by Janice Glime.

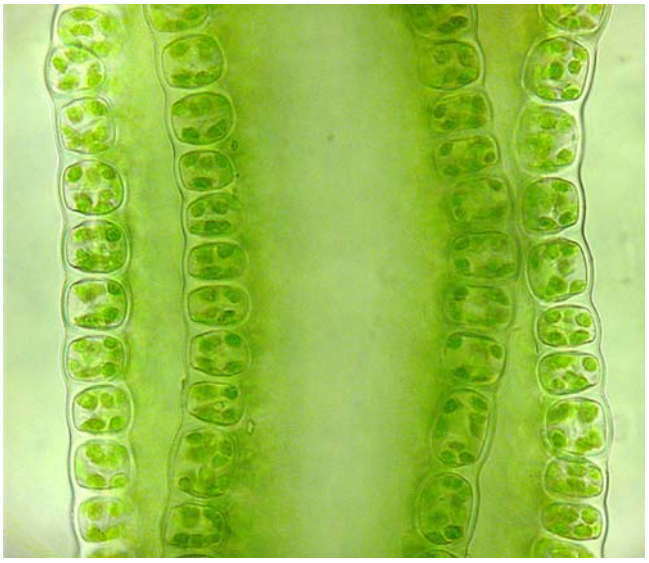

Figure 20. ***Atrichum undulatum*** leaf showing tips of lamellae. Photo by Walter Obermayer, with permission.

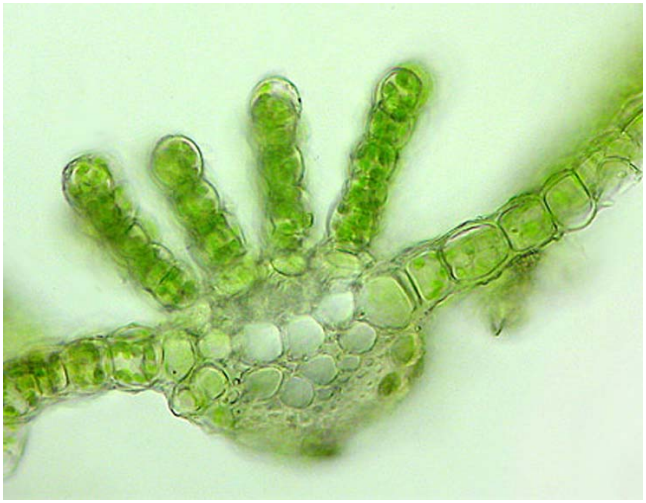

Figure 21. ***Atrichum undulatum*** leaf cross section showing lamellae. This moss has little or no wax on its leaves. Photo by Walter Obermayer, with permission.

Figure 22. ***Atrichum altecristatum*** drying (**lower part of image**). Photo by Eric Schneider, with permission.

Figure 23. ***Atrichum undulatum*** leaf lamellae and out of focus areas that indicate undulations. Photo by Walter Obermayer, with permission.

The array of species with demonstrated waxes is a mixed group of xerophytes and hydrophytes (Proctor 1979b, 1982). ***Pohlia wahlenbergii*** (Figure 24-Figure 26), a glaucous moss of wet habitats, has a high content of wax, whereas ***Pohlia nutans*** (Figure 27-Figure 28), a ubiquitous moss often found in dry habitats, has little wax. ***Pohlia cruda*** (Figure 29-Figure 31), a species of moist places, has a high content like that of ***P. wahlenbergii***. It appears that the wax in these species is important to prevent water logging, allowing for gas exchange for photosynthesis.

Figure 24. ***Pohlia wahlenbergii*** showing a wet habitat that is typical for it. Photo by Michael Lüth, with permission.

Figure 25. ***Pohlia wahlenbergii*** showing water droplets that are repelled by the waxy surface. Photo by Michael Lüth, with permission.

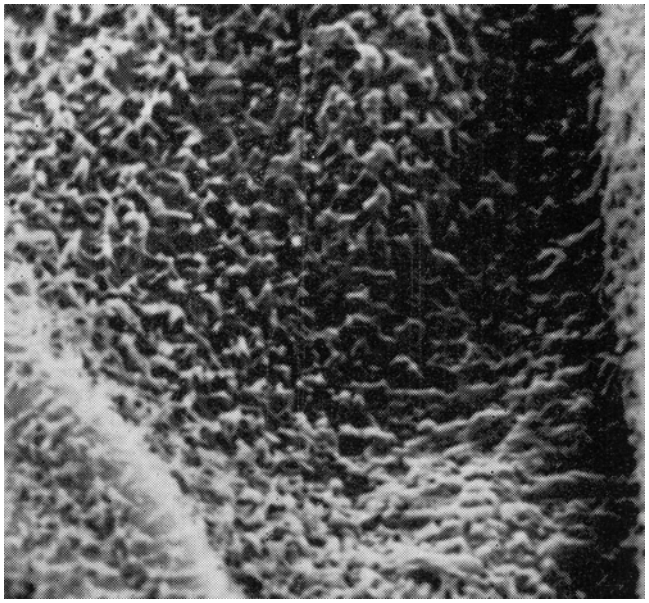

Figure 26. SEM of ***Pohlia wahlenbergii*** cuticle. Photo by Michael Proctor, with permission.

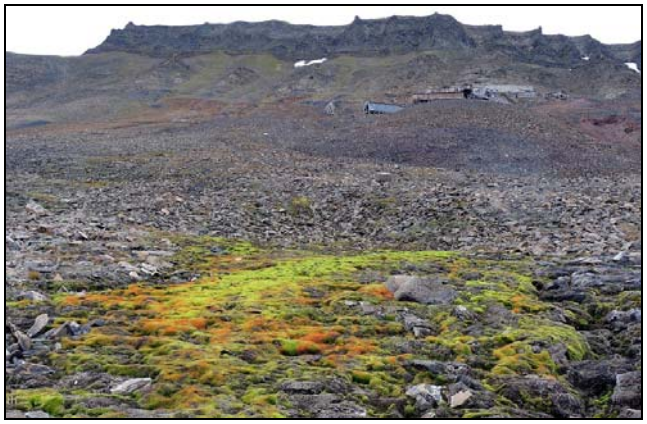

Figure 27. ***Pohlia nutans*** showing a typical dry, exposed habitat for the species. Photo by Michael Lüth, with permission.

Figure 28. ***Pohlia nutans*** showing the lack of a glaucous or waxy appearance. Photo by Michael Lüth, with permission.

Figure 29. ***Pohlia cruda*** in a crevice where moisture can be maintained, showing a waxy appearance. Photo by Michael Lüth, with permission.

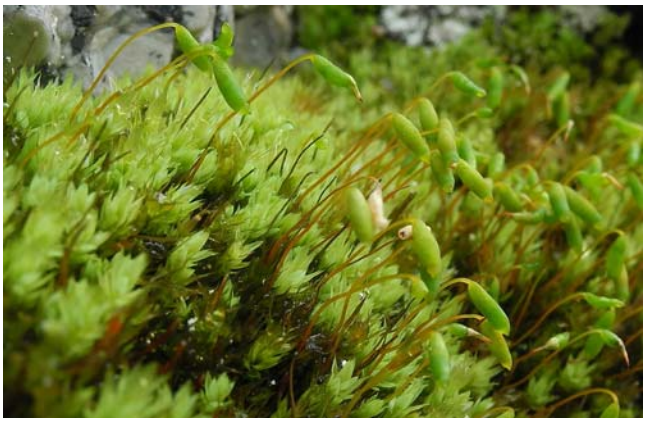

Figure 30. ***Pohlia cruda***, a glaucous moss with a high leaf wax content. Photo by Michael Lüth, with permission.

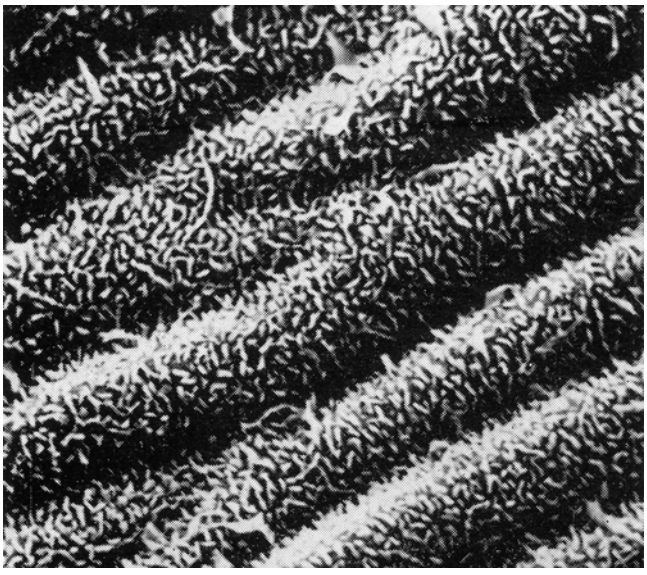

Figure 31. SEM of ***Pohlia cruda*** cuticle. Photo by Michael Proctor, with permission.

Bartramia pomiformis (Figure 32-Figure 34) has a whitish appearance and has a high degree of wax covering (Figure 34) (Proctor 1979b). In the same family, ***Conostomum tetragonum*** (Figure 35) has an intriguing 3-d mesh of wax (Figure 36).

Figure 32. ***Bartramia pomiformis*** in its typical rock crag habitat. Photo by Janice Glime.

Figure 33. ***Bartramia pomiformis*** showing glaucous leaves. Photo by Michael Lüth, with permission.

Figure 34. SEM of ***Bartramia pomiformis*** leaf cuticle. Photo by Michael Proctor, with permission.

Figure 35. ***Conostomum tetragonum*** showing the glaucous appearance of the leaves. Photo by Des Callaghan, with permission.

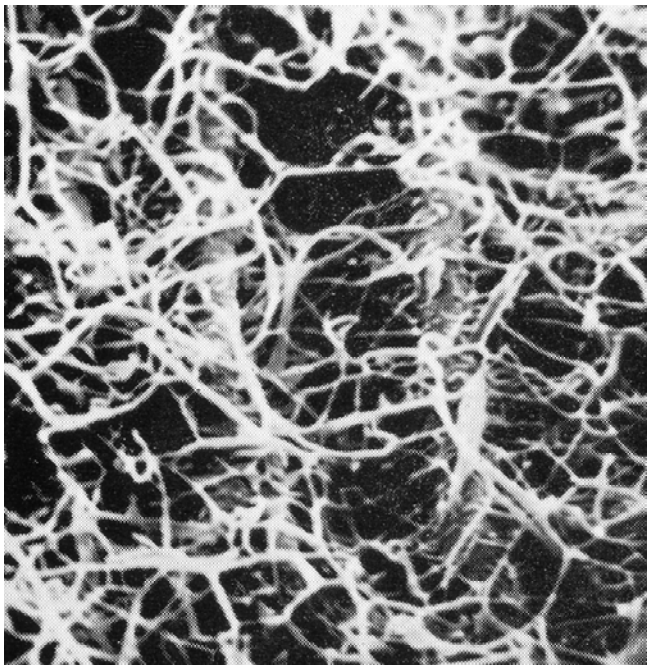

Figure 36. SEM of ***Conostomum tetragonum*** leaf cuticle. Photo by Michael Proctor, with permission.

Xu *et al*. (2009) found surface wax on the leaves of the desert moss ***Syntrichia caninervis*** (Figure 37). These waxes were comprised of fatty acids, alcohols and alkanes. In this species, the wax crystals shift as the leaf ages, increasing the percentage and weight (13.6%; 1150 μg g^{-1} DW) of very long-chain components in young leaves to 37.2% and 2640 μg g^{-1} in older leaves. Furthermore, when juvenile leaves experienced dehydration followed by rehydration the wax content of juvenile leaves increased by 35.17%. In lab-cultivated leaves subjected to three wet/dry cycles, the wax content increased by 1900%.

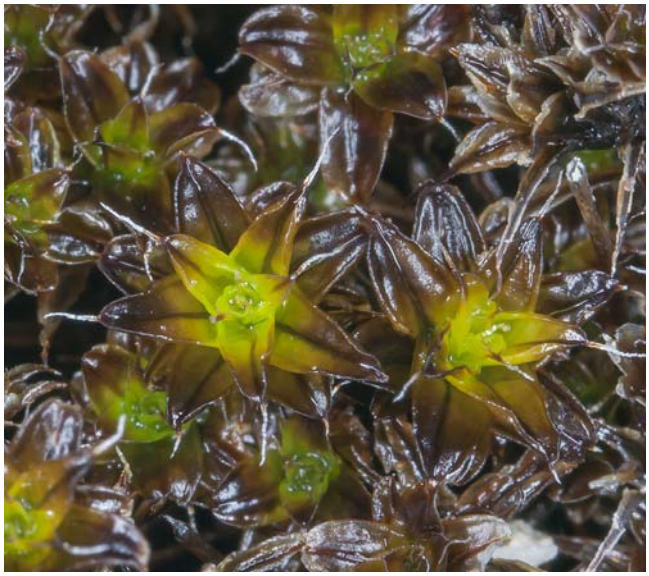

Figure 37. ***Syntrichia caninervis***, a desert moss with a cuticle comprised of fatty acids, alcohols, and alkanes. Photo by John Game, with permission.

Some bryophytes are puzzling at first glance. For example, ***Hedwigia*** (Figure 38-Figure 40) species appear to be waxy, yet absorb water rapidly. But members of the **Hedwigiales** lack waxes (Pressel & Duckett 2011). This puzzle unravels when we understand the role of the papillae (which typically make leaves look whitish) on the leaves of **Andreaeales**, **Grimmiales** (Figure 41-Figure 42), **Pottiales** (Figure 43-Figure 46), **Hedwigiales**, and **Orthotrichales**. Based on experiments by Proctor (1979a) and confirmed by Pressel and Duckett (2011), the water enters these leaves by flowing within channels in the **striated** (having linear marks, slight ridges, or grooves on surface, often one of number of similar parallel features) cell walls and between the papillae, causing rapid uptake of water through the leaf surface between the papillae. These taxa lack waxes.

Figure 38. ***Hedwigia ciliata ciliata*** dry, showing whitish leaves resulting from numerous papillae. Photo by Des Callaghan, with permission.

Figure 39. ***Hedwigia ciliata*** wet, showing ability to spread when hydrated. Photo by Hermann Schachner, through Creative Commons.

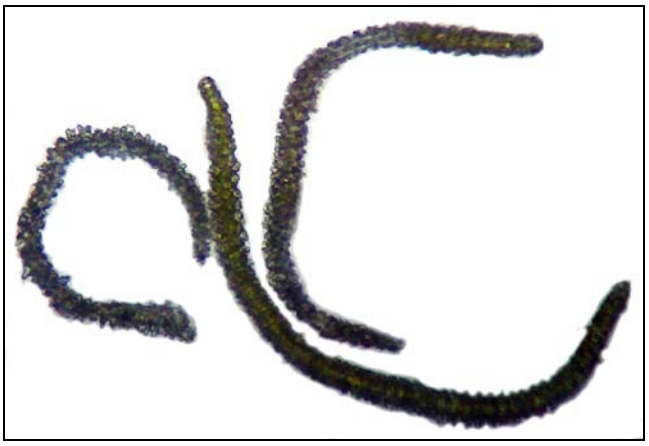

Figure 40. ***Hedwigia ciliata*** leaf cross sections showing dense papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 41. ***Racomitrium lanuginosum*** (**Grimmiales**) showing awns on leaves. These leaves lack waxes. Photo from Botany Department website, University of British Columbia, with permission.

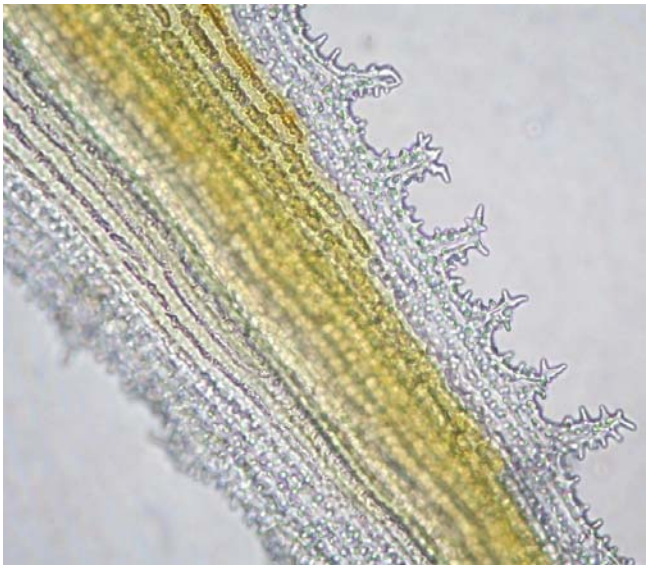

Figure 42. ***Racomitrium lanuginosum*** (**Grimmiales**) leaf awn and cell papillae. Photo from Botany Department website, University of British Columbia, with permission.

Figure 43. ***Tortula muralis*** in its dry state. Photo by Christophe Quintin, through Creative Commons.

Figure 44. ***Tortula muralis*** in its wet state. Note the water collected on the awns. Photo by Christophe, Quintin through Creative Commons.

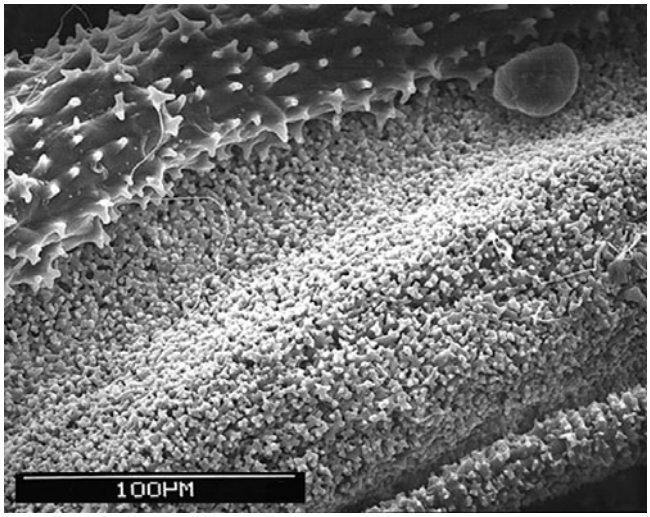

Figure 45. SEM of ***Tortula muralis*** (**Pottiales**) papillae showing their density and channels where water moves and enters the leaf. Photo from Botany Department website, University of British Columbia, with permission.

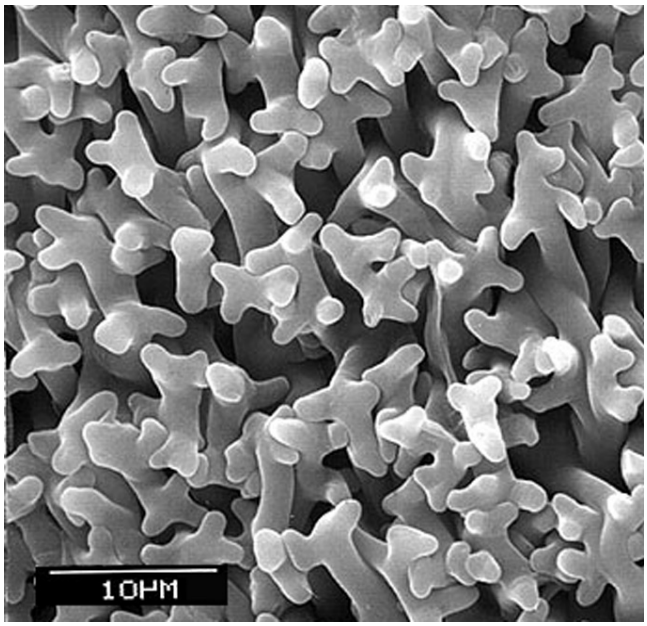

Figure 46. SEM of ***Tortula muralis*** (**Pottiales**) papillae showing the spaces between them where channels are provided for water transport and entry to the leaf cells. Photo from Botany Department website, University of British Columbia, with permission.

In genera such as ***Aloina*** (Figure 47), ***Crossidium*** (Figure 48-Figure 49), and ***Pterygoneurum***, (Figure 50-Figure 52) the water enters between the leaf lamellae (Figure 51-Figure 52) (Proctor 1979a; Pressel & Duckett 2011). All these taxa grow in habitats where intermittent dehydration/rehydration, often in rapid sequence, is common. However, in the **Polytrichaceae** (Figure 14-Figure 18), water logging between the lamellae is an issue, depressing gas exchange needed for photosynthesis (Proctor 1979a, 1982, 1984). These leaves are protected by abundant waxes that prevent water from entering the spaces between the leaf lamellae. Instead, air bubbles are trapped in these spaces.

Figure 47. ***Aloina rigida*** showing waxy leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 48. ***Crossidium aberrans*** leaves with lamellae. Photo by Michael Lüth, with permission.

Figure 49. ***Crossidium aberrans*** leaf cells showing lamellae in center where water is easily absorbed. Photo by Michael Lüth, with permission.

Figure 50. ***Pterygoneurum papillosum*** showing succulent appearance of leaves due to lamellae. Photo by Michael Lüth, with permission.

Figure 51. ***Pterygoneurum ovatum*** leaf showing lamellae where water enters the leaf. Photo by Hermann Schachner, through Creative Commons.

Figure 52. ***Pterygoneurum ovatum*** leaf cross section showing lamellae where water enters leaf. Photo by Hermann Schachner,through Creative Commons.

One of the problems that bryophytes must face is having ice or ice crystals on their surfaces (Figure 53-Figure 54). These crystals are very hygroscopic, potentially causing the kind of dehydration that can occur to your meat in the freezer. A waxy cuticle could serve like a plastic freezer bag, in this case preventing the water from being drawn from the cells. This role for the wax, if present, remains to be tested.

Figure 53. ***Polytrichum*** sp. with frost, a condition that could draw water out of unprotected cells. Photo by Allan Water.

Figure 54. ***Hedwigia ciliata*** in ice, a frequent condition for this rock dweller. The ice, like freezer ice, draws water out of plant cells. Photo by Michael Lüth, with pernission.

The presence of a white flocculent material on the moss ***Saelania glaucescens*** (Figure 55-Figure 57) is widely known. ***Saelania glaucescens*** has been a puzzle to bryologists and biochemists. Its whitish covering is predominantly on the backs of the leaves and takes the form of a hoary appearance, not a smooth or shiny surface. Although this material has been identified as kauranol plus several minor waxes (Nilsson & Mårtensson 1971), the reason for the peculiar arrangement that looks like a thin layer of minute angel hair remains a mystery. Bryologists have suggested that it might be caused by parasitic fungi or bacteria, but there is no evidence to support these ideas (Mårtensson & Nilsson 1974). Likewise, it does not seem to be the result of any normal metabolic product. Proctor's (1979b) analysis demonstrates that this is a heavy coating of waxes with weblike ridges covered by a fine, cobwebby matrix of wax.

Figure 55. ***Saelania glaucescens*** showing waxy appearance. Photo by Michael Lüth, with permission.

Figure 56. ***Saelania glaucescens***, a moss in which the waxy extrusions are so large that they are visible to the naked eye. Photo by Jan-Peter Frahm, with pernission.

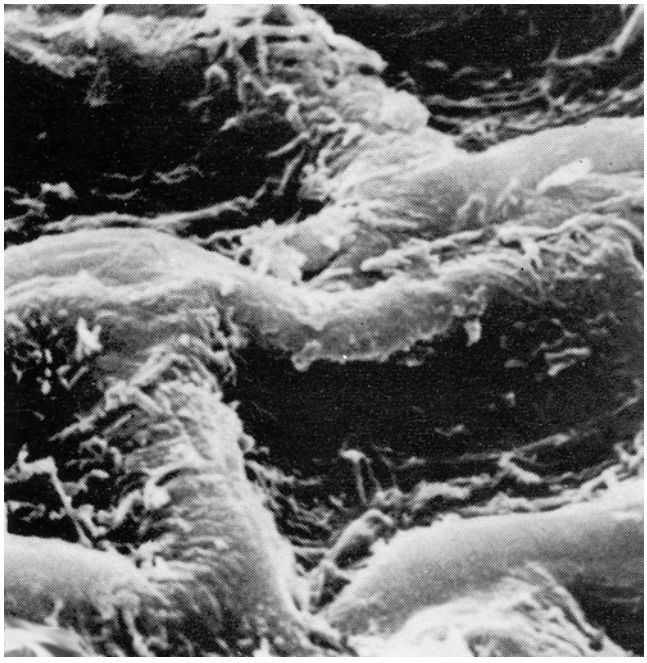

Figure 57. SEM of ***Saelania glaucescens*** cuticle. Photo by Michael Proctor, with pernission.

Sphagnum

Sphagnum fimbriatum (Figure 58-Figure 62), a peatmoss of wet habitats, has an osmiophilic layer (one that stains with osmium tetroxide, indicating wax) that resembles the early developmental stage of tracheophyte cuticle (Cook & Graham 1998). One might think that a wet habitat moss would not need such protection, but in summer these peatmosses can become quite dry, so such a layer may help to reduce desiccation. On the other hand, this layer may prevent water logging at times when this moss is submersed (*cf*. Pressel & Duckett 2011). The cuticle in ***S. fimbriatum*** is sheetlike with regular ridges that run parallel to the edges of the "thalli." Our next question is how can a leaf with a cuticle use it for protection from desiccation and yet be able to absorb water. In ***Sphagnum***, this may be facilitated by the pores, but might the structure of the cuticle play a role?

Figure 58. Dry ***Sphagnum fimbriatum***, a moss with a known osmiophilic layer resembling an early developmental cuticle of tracheophytes. Photo by Michael Lüth, with pernission.

Figure 59. ***Sphagnum capillaceum*** (= *S. nemoreum*), a ***Sphagnum*** species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with pernission.

Figure 60. ***Sphagnum fuscum***, a ***Sphagnum*** species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with pernission.

Figure 61. ***Sphagnum magellanicum***, a species known to have waxes. Photo by Michael Lüth, with pernission.

Figure 62. ***Sphagnum fimbriatum*** leaf cross section, a moss that has an osmiophilic (waxy) layer on the outside of the leaf cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with pernission.

Leafy Liverworts

Even the leafy liverworts can have waxes. Heinrichs *et al*. (2000) support the contention of Cook and Graham (1998) that this innovation occurred prior to the evolution of bryophytes from their algal ancestor. Although only six (5 of ***Plagiochila*** plus ***Plagiochilion mayebarae***) of the 81 species of **Plagiochilaceae** in the study had surface waxes on their leaves (Heinrichs *et al*. 2000), this is a family with

many members in damp or wet, even submersed, habitats. They found that ***P. tabinensis*** contains 1.4% of its dry weight as surface waxes. These are comprised of steryl esters, triacylglycerols, and free fatty acids.

By using the electron microscope, Heinrichs and Reiner-Drehwald (2012) found surface wax in the leafy liverworts ***Lejeunea flava*** (Figure 63), ***Mytilopsis albifrons***, ***Dinckleria pleurata***, and ***D. fruticella***, representing the families **Lejeuneaceae**, **Lepidoziaceae**, and **Plagiochilaceae**, respectively.

Figure 63. ***Lejeunea flava***, a leafy liverwort known to have a cuticle with surface wax. Photo by Jonathan Sleath, with pernission.

Admissibility of Water

If leaves of bryophytes are covered with waxes, how does water enter these largely ectohydric plants? One suggestion is that the bases of the leaves may lack a cuticle, but that would seem to slow down water entry and be maladaptive for gathering dew or taking advantage of short desert rainfall events. But the structure of the wax itself may solve this problem. Shepherd and Wynne Griffiths (2006) describe the layered sheets of wax as probably discontinuous and surrounded by further solid amorphous regions. The crystalline regions are considered impermeable, but water and solutes are able to diffuse through the cuticular wax by way of the amorphous zones. This requires a greater travel distance than a straight path through the surface, but it seems a better route than travelling to the leaf base, then travelling internally through cell contents and cell walls to reach the tip of the leaf.

Multiple Forms – Multiple Roles

The cuticle, like many plant features, can serve multiple advantages for plants. In tracheophytes it is able to reduce water loss, prevent water logging, protect against high light intensity, reduce the temperature, reduce osmotic stress, prevent physical damage, protect against altitudinal stresses (light, extreme temperatures, wind), and protect against pollution (Shepherd & Wynne Griffiths 2006).

In tracheophytes, waxes exist in several forms, including rods, ribbons, filaments, tubes, and plates (Shepherd & Wynne Griffiths 2006). Among the bryophytes, for five ***Plagiochila*** (leafy liverwort) species studied, two exhibited wax platelets and three exhibited wax rodlets (Heinrichs *et al*. 2000). Proctor (1979b) demonstrated several forms among mosses (Figure 31, Figure 34, Figure 36, Figure 57).

Among the tracheophyte forms, wax tubes are associated with mid-chain oxy-substituents, such as β-diketones, hydroxy-β-diketones, diols, and secondary alcohols (Shepherd & Wynne Griffiths 2006). Platelets are associated with primary alcohols with a terminal oxy-substituent. Are these same factors influential in bryophyte wax morphology? If so, is there any adaptive significance for these differences?

Temperature

We know that in tracheophytes temperature, light intensity, and humidity influence the wax morphology, but since these three factors typically act together, it is often difficult to tease out cause and effect (Shepherd & Wynne Griffiths 2006). For example, in *Citrus aurantium*, a higher daytime temperature during leaf development reduces the quantities of alkanes, primary alcohols, fatty acids, and alkyl esters per unit area (Riederer & Schneider 1990). But except for the esters, the amounts of these same compounds increase with higher night-time temperatures.

At higher temperatures, the waxes are more likely to form plates and flakes, whereas at lower temperatures they are more likely to form vertical structures such as rods and tubes (Shepherd & Wynne Griffiths 2006). But waxes at higher temperatures also often form complex dendritic shapes. Tubular forms of waxes are thermodynamically unstable due to their high surface area to volume ratio, so an input of energy, typically heat, can transform them into compact planar forms that are thermodynamically more stable. And tubes can turn into dendrites when the temperature is raised. On the other hand, rapid cooling can also favor dendrite formation. Furthermore, more waxes are produced at lower temperatures.

Light

Shorter, less elaborate wax structures are often associated with greater illumination (Shepherd & Wynne Griffiths 2006). Thick waxes such as those in *Eucalyptus* leaves increase reflectance and reduce photosynthesis, but in "non-waxy" leaves (*i.e.* not appearing waxy or glaucous), there is no effect. In wheat, reflectance is proportional to the amount of wax present, with higher reflectance reducing light transmission to underlying mesophyll cells (Johnson *et al*. 1983). Higher radiation levels can cause an increase in wax thickness in many plants, suggesting an inducible mechanism to protect the cells (Baker 1974; Giese 1975; Reed & Tukey 1982; Shepherd *et al*. 1995).

But it seems unlikely that the thin cuticle of bryophytes has much of an effect on reflectance or photosynthesis. Nevertheless, as will be seen in the chapter on light relations, many bryophyte leaves transmit more light when wet than when dry, suggesting that papillae or other surface features may screen light, thus protecting the DNA and chlorophyll, but that when water fills in the spaces, light is transmitted rather than scattered. Are these waxes protective agents against UV radiation when the

bryophytes are dry? But UV reflectance is an uncommon adaptation among tracheophytes. It can range from <10% in most plant species, to 70% in only a few others (Caldwell *et al.* 1983; Barnes *et al.* 1996).

Waxes may play yet another role for the light-limited bryophytes. Droplets held on wettable tracheophyte leaves can focus solar radiation up to 20 times (Brewer *et al.* 1991). We might imagine that bryophyte leaves or multiple plant tips might trap water droplets that likewise focus the light in some low-light habitats. This focussing would occur at the actively growing tips in most acrocarpous mosses.

Salt Stress

Waxes also protect leaf cells from salt stress (Shepherd & Wynne Griffiths 2006). Examples from tracheophytes suggest that an increase in wax production may be an inducible response to increased salt exposure. Fujiwara *et al.* (2002) found that pre-treating cabbage seedlings with NaCl induced hardening, improving drought resistance. It would be interesting to compare wax content among bryophytes that grow within areas affected by salt spray to the same species grown away from its influence.

Contact Angles and Entry

Contact angles are important for water entry. Brewer *et al.* (1991) found that changes in the contact angle and wettability are also associated with changes in wax composition and morphology in tracheophytes. These observations present interesting questions for bryophytes. If leaves have waxes over the leaf lamina, but lack waxes at the base, water will roll to the leaf base where uptake is easy. This movement to the leaf base would further facilitate the solution of deposited nutrients and carry them to the base for absorption (Cape 1996 for tracheophytes). Because of the mode of water uptake in bryophytes, this feature is likely to be more important than it is in tracheophytes. Hence, we should expect the angle of the leaf to be important in this nutrient and water gathering. At the same time, it presents dangers for collecting deposited pollutants.

Combined Role and Water Relations

Let's continue under the assumption that at least in some cases the waxes on bryophytes may play a role in reflectance and scattering of light to a degree that can lower the temperature of the bryophyte cells they cover. This will, in turn, reduce the vapor pressure difference between the leaf tissue and the air, reducing the loss of water through transpiration. But all these assumptions remain to be tested in bryophytes.

Altitude Protection

High altitude imposes stresses that include weathering, dehydration, low temperatures, and greater UV light intensity. In conifers, a thicker wax coverage is characteristic of high altitude growth (Günthardt 1984; Riolo 1999). We need to look for a similar relationship in bryophytes.

Pollution Protection

Ozone

In tracheophytes, ozone causes a severe reduction in the formation of new wax, but it does not seem to affect existing wax (Carlsson *et al.* 1994; Hellgren *et al.* 1995). Its effect on bryophyte cuticles remains unknown, but failure to replace cuticle could have severe consequences in prevention of water logging and protection from UV radiation.

CO_2

The effects of CO_2 on tracheophytes are varied, in some cases causing an increase in waxes and in others a decrease (Shepherd & Wynne Griffiths 2006). The effect on bryophyte cuticles remains to be demonstrated.

Repelling Water

Despite all of these reports on waxes on the cuticle of bryophytes, we know little of their role. Mårtensson and Nilsson (1974) comment that not all of the aforementioned waxy species are shiny, including ***Rhytidiadelphus triquetrus*** (Figure 9), although I would consider it to be shiny. Others, such as ***Sphagnum subnitens*** (Figure 64-Figure 65) and ***S. subfulvum*** (Figure 66) are shiny when dry, but lose their shine when moist, suggesting that the relationship is complex and is not a matter of simple reflection. It would be interesting to determine their role in repelling water to avoid water logging vs retaining water in times of drought.

Figure 64. ***Sphagnum subnitens*** dry with a waxy shine. Photo by Michael Lüth, with pernission.

Figure 65. ***Sphagnum subnitens*** wet with a less waxy look than dry plants. Photo by Barry Stewart, with pernission.

Figure 66. ***Sphagnum subfulvum***, a species that is shiny when dry due to waxes. Photo by Michael Lüth, with pernission.

The role of repelling water may be more important than that of retaining water. I have mentioned a potential role of repelling water, as seen in Figure 1. Gas exchange works poorly through a wet surface. Waxy or oily surfaces help to repel the water, yet allow a higher rate of gas exchange than does water. Hence it is not uncommon to find such surfaces among aquatic bryophyte taxa (Proctor 1984).

Proctor (1984) contends that the ability to shed surface water is important to bryophytes in their low-light habitats of crevices and caves or in waterside habitats of waterfalls. He cites the waxy surfaces of the tops of photosynthetic lamellae of the **Polytrichaceae** (Figure 6, Figure 14-Figure 18) as support for this contention. This might also be supported by the waxy surface of ***Pohlia cruda*** (Figure 29-Figure 31), a common species in crevices.

As discussed in Chapter 7-3 of this volume, the pores of ***Marchantia*** (Figure 67), as in the stomata of tracheophytes, have strongly water-repellent ledges (Schönherr & Ziegler 1975; Figure 68), like the waxy ridges of tracheophytes, preventing water from entering and interfering with the photosynthetic interior.

Figure 67. ***Marchantia polymorpha*** with gemmae cups and tiny white dots that indicate pores. Photo by Jan-Peter Frahm, with pernission.

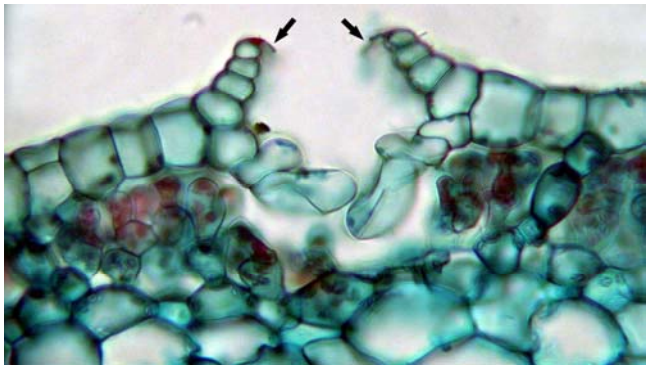

Figure 68. Section through pore of ***Marchantia polymorpha***, with waxy ledge indicated by arrows. Photo by George Shepherd, through Creative Commons.

Mosses like ***Plagiomnium*** (Figure 69) have both upright and horizontal stems. But this genus has a different problem from most mosses in obtaining water. Its leaves repel water, as known by anyone who has tried to wet them to make a slide. It has perhaps solved this problem by its well-developed hydroids and leptoids, and even false leaf traces (Figure 70).

Figure 69. ***Plagiomnium ellipticum*** with drops of water on its water-repellent (waxy) surface. Photo by Des Callaghan, with pernission.

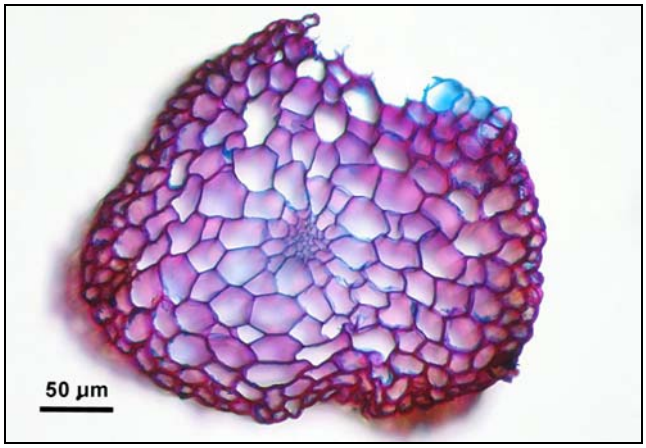

Figure 70. ***Plagiomnium ellipticum*** stem cross section. This is a moss with both upright and horizontal (plagiotropic) stems. It most likely benefits from having both hydroids and leptoids to transport substances because its leaves are very resistant to getting wet and typically repel water. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with pernission.

In some cases, there are special adaptations for bringing water into the leaves while at the same time being able to prevent water loss. In ***Rhacocarpus purpurascens*** (Figure 71), a moss of exposed habitats that experience frequent alternation of drought and heavy precipitation, the cell walls are trilamellate (Pressel *et al*. 2010). The outer layer is porous and ensures rapid uptake of water and retention. At the same time its very hydrophobic cuticle-like layer prevents waterlogging. The middle lamellar stratum permits extension of protoplast hydration, allowing the metabolism to remain active under drying conditions. ***Sphagnum***, on the other hand, can become waterlogged and experience depressed metabolism as a result.

Figure 71. ***Rhacocarpus purpurascens***, a moss that repels water. Photo by Michael Lüth, with pernission.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves**, **concave leaves**, **crispate leaves**, **plications**, **revolute** or **involute margins**, **lamellae**, **multi-layered leaves**, **lobules, cuticles**, **hair points**, **papillae**, **costae**, **stereids**, **borders**, **cancellinae**, **teniolae**, **alar cells**, **hyaline cells**, **pores**, **oil bodies**, **vacuoles** aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Waxes are known from all the major groups of bryophytes, including such aquatic taxa as ***Sphagnum***, and occur in a wide range of habitat moisture, but many species seem to lack them. Glaucous species may be so because of waxes or because of dense papillae. The water repellant nature of waxes keeps water from entering pores of a thallus and prevents water from remaining on plants in a way that blocks gas exchange. The presence of waxes may relate to endohydry or to living in places where water lingers on the plants. The role may be more to keep water away than to hold water in.

Waxes need to be arranged on a leaf to admit water, at least at the base, but they may have an amorphous layer that transmits water. Multiple forms of waxes seem to be correlated with various environmental parameters such as UV light, temperature, salt stress, contact angle, and altitude, but these correlations have not been explored in bryophytes. Cuticles can offer protection from such pollutants as ozone and CO_2 and may play a role in preventing absorption of airborne pollutants that land on the surfaces of the leaves.

Acknowledgments

An earlier version of this chapter benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. Translation of part of the work by Loeske was by Ron Gratz. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. I was fortunate to have Ken Kellman ask on Bryonet for examples of bryophytes with a demonstrated cuticle; he was kind enough to share his collected references with me and offer suggestions for improving this chapter.

Literature Cited

Baker, E. A. 1974. The Influence of environment on leaf wax development in *Brassica oleracea* var. *gemmifera*. New Phytol. 73: 955-966.

Barnes, J. D., Percy, K. E., Paul, N. D., Jones, P., McLaughin, C. K., Mullineaux, P. M., Creissen, G., and Wellburn, A. R. 1996. The influence of UV-B radiation on the physiochemical nature of tobacco (*Nicotiana tabacum* L.) leaf surfaces. J. Exper. Bot. 47: 99-109.

Brewer, C. A., Smith, W. K., and Vogelmann, T. C. 1991. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. Plant Cell Environ. 14: 955-962.

Buda, G. J., Barnes, W. J., Fich, E. A., Park, S., Yeats, T. H., Zhao, L., Domozych, D. S., and Rose, J. K. 2013. An ATP binding cassette transporter is required for cuticular wax deposition and desiccation tolerance in the moss *Physcomitrella patens*. Plant Cell Online 25: 4000-4013.

Caldwell, M. M., Robberecht, R., and Flint, S. D. 1983. Internal filters: Prospects for UV-acclimation in higher plants. Physiol. Plant. 58: 445-450.

Cape, J. N. 1996. Surface wetness and pollutant deposition. In: Kerstiens, G. (ed.). Plant Cuticles. An Integrated Functional Approach. BIOS Scientific Publishers Ltd., Oxford, UK, pp. 283-300.

Carlsson, A. S., Hellgren, L. I., Selldén, G., and Sandelius, A. S. 1994. Effects of moderately enhanced levels of ozone on the acyl lipid composition of leaf lipids of garden pea (*Pisum sativum*). Physiol. Plant. 91: 754-762.

Cook, M. E. and Graham, L. E. 1998. Structural similarities between surface layers of selected charophycean algae and bryophytes and the cuticles of vascular plants. Internat. J. Plant Sci. 159: 780-787.

Fujiwara, T., Nakayama, M., Kikuchi, S., Yoshioka, H., and Sato, F. 2002. Applying NaCl to suppress succulent growth and acclimatize cabbage plug seedlings. J. Jap Soc. Hort. Sci 71: 796 804.

Giese, B. N. 1975. Effects of light and temperature on the composition of epicuticular wax of barley leaves. Phytochemistry 14: 921-929.

Günthardt, M. S. 1984. Epicuticular wax of *Picea abies* needles. In: Sigenthaler, P.-A. and Eichenberger, W. Structure, Function and Metabolism of Plant Lipids. Elsevier, Amsterdam, Netherlands, pp. 499-502.

Haas, K. 1982. Surface wax of *Andreaea* and *Pogonatum* species. Phytochemistry 21: 657-659.

Heinrichs, J. and Reiner-Drehwald, E. 2012. Surface Wax in *Dinckleria*, *Lejeunea* and *Mytilopsis* (Jungermanniidae). Cryptog. Bryol. 33: 81-86.

Heinrichs, J. H., Anton, H., Gradstein, S. R., Mues, S. R., and Holz, I. 2000. Surface wax, a new taxonomic feature in Plagiochilaceae. Plant Syst. Evol. 225: 225–233.

Hellgren, L. I., Carlsson, A. S., Selldén, G., and Sandelius, A. S. 1995. *In situ* leaf metabolism in garden pea (*Pisum sativum* L.) exposed to moderately enhanced levels of ozone. J. Exper. Bot. 46: 221-230.

Howard, J. A. 1967. Spectral energy relations of isobilateral leaves. Austral. J. Biol. Sci. 19: 757-766.

Ives, D. A. J. and O'Neill, A. N. 1958. The chemistry of peat. Can. J. Chem. 36: 926-930.

Johnson, D. A., Richards, R. A., and Turner, N. C. 1983. Yield, water relations, gas exchange, and surface reflectance of near-isogenic wheat lines differing in glaucousness. Crop Sci. 24: 318-325.

Mårtensson, O. and Nilsson, E. 1974. On the morphological colour of mosses. Lindbergia 2: 143-159.

Nilsson, E. and Mårtensson, O. 1971. Chemical studies on bryophytes 11. (-)-16α-Hydroxykaurane from *Saelania glaucescens* (Hedw.) Broth. Acta Chemica Scandinavica 25: 1486-1487.

Pressel, S. and Duckett, J. 2011. Bryophyte surfaces; New functional perspectives from Cryo-Scanning Electron Microscopy. Field Bryol. 104: 50-53.

Pressel, S., P'ng, K. M. Y., and Duckett, J. G. 2010. A cryo-scanning electron microscope study of the water relations of the remarkable cell wall in the moss *Rhacocarpus purpurascens* (Rhacocarpaceae, Bryophyta). Nova Hedwigia 91: 289-299.

Proctor, M. C. F. 1979a. Structure and eco-physiological adaptations in bryophytes. In: Clarke, G. C. S. and Duckett, J. G. (eds.). Bryophyte Systematics, Systematic Association special volume 14, Academic Press, London, pp. 479-509.

Proctor, M. C. F. 1979b. Surface wax on the leaves of some mosses. J. Bryol. 10: 531-538.

Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology, Chapman and Hall, London, pp. 333-381.

Proctor, M. C. F. 1984. Structure and ecological adaptation. In: Dyer, A. F. and Duckett, J. G. (eds.). The Experimental Biology of Bryophytes, Academic Press, London, pp. 9-37.

Reed, D. W. and Tukey, H. B. Jr. 1982. Light intensity and temperature effects on epicuticular wax morphology and internal cuticle ultrastructure of carnation and Brussels sprouts leaf cuticles. J. Amer. Hort. Sci. 107: 417-420.

Riederer, M. and Schneider, G. 1990. The effect of environment on the permeability and composition of citrus leaf cuticles. Planta 180: 154-165.

Riolo, A. 1999. Variazioni stagionali di alcuni componenti fogliari in *Picea abies* (L.) Karst, durante l'acclimatazione al freddo. M.Sc. Thesis, University of Padova, Italy.

Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. Planta, Berlin 124: 51-60.

Shepherd, T., Robertson, G. W., and Griffiths, D. W. 1995. Compositional analysis of intact alkyl esters in leaf epicuticular wax of swede by capillary gas chromatography and electron-impact mass spectrometry. Phytochem. Anal. 6: 65-73.

Shepherd, T. and Wynne Griffiths, D. 2006. The effects of stress on plant cuticular waxes. New Phytol. 171: 469-499.

Stránsky, K., Streibl, M., and Herout, V. 1967. On natural waxes. VI. Distribution of wax hydrocarbons in plants of different evolutionary levels. Coll. Czechoslov. Chem. Comm. 32: 3213-3220.

Xu, S. J., Jiang, P. A., Wang, Z. W., and Wang, Y. 2009. Crystal structures and chemical composition of leaf surface wax depositions on the desert moss *Syntrichia caninervis*. Biochem. Syst. Ecol. 37: 723-730.

CHAPTER 7-5

WATER RELATIONS: PHYSIOLOGICAL ADAPTATIONS

TABLE OF CONTENTS

Water Relations on Land 7-5-2
Drought Tolerance vs Avoidance 7-5-3
    Desiccation Tolerance 7-5-4
    Desiccation Avoidance 7-5-9
Life Cycle and Life Strategy Adaptations 7-5-9
Seasonal Changes 7-5-11
Physiological Adaptations 7-5-14
    Mode of Conduction 7-5-16
    Osmotic Potential and Turgor 7-5-21
        Water Content 7-5-24
        Water-logging 7-5-26
    Inducible vs Constitutive Desiccation Tolerance 7-5-26
        Hardening 7-5-28
    Desiccation-induced Changes 7-5-28
        Cell Contents 7-5-30
        Chloroplast Responses 7-5-31
        Photosynthesis 7-5-31
        Mitochondria 7-5-32
        Nuclei 7-5-32
        Vacuoles and Vesicles 7-5-32
        Membranes 7-5-32
        Plasmolysis 7-5-33
        Liverworts 7-5-33
Summary 7-5-34
Acknowledgments 7-5-34
Literature Cited 7-5-34

CHAPTER 7-5

WATER RELATIONS: PHYSIOLOGICAL ADAPTATIONS

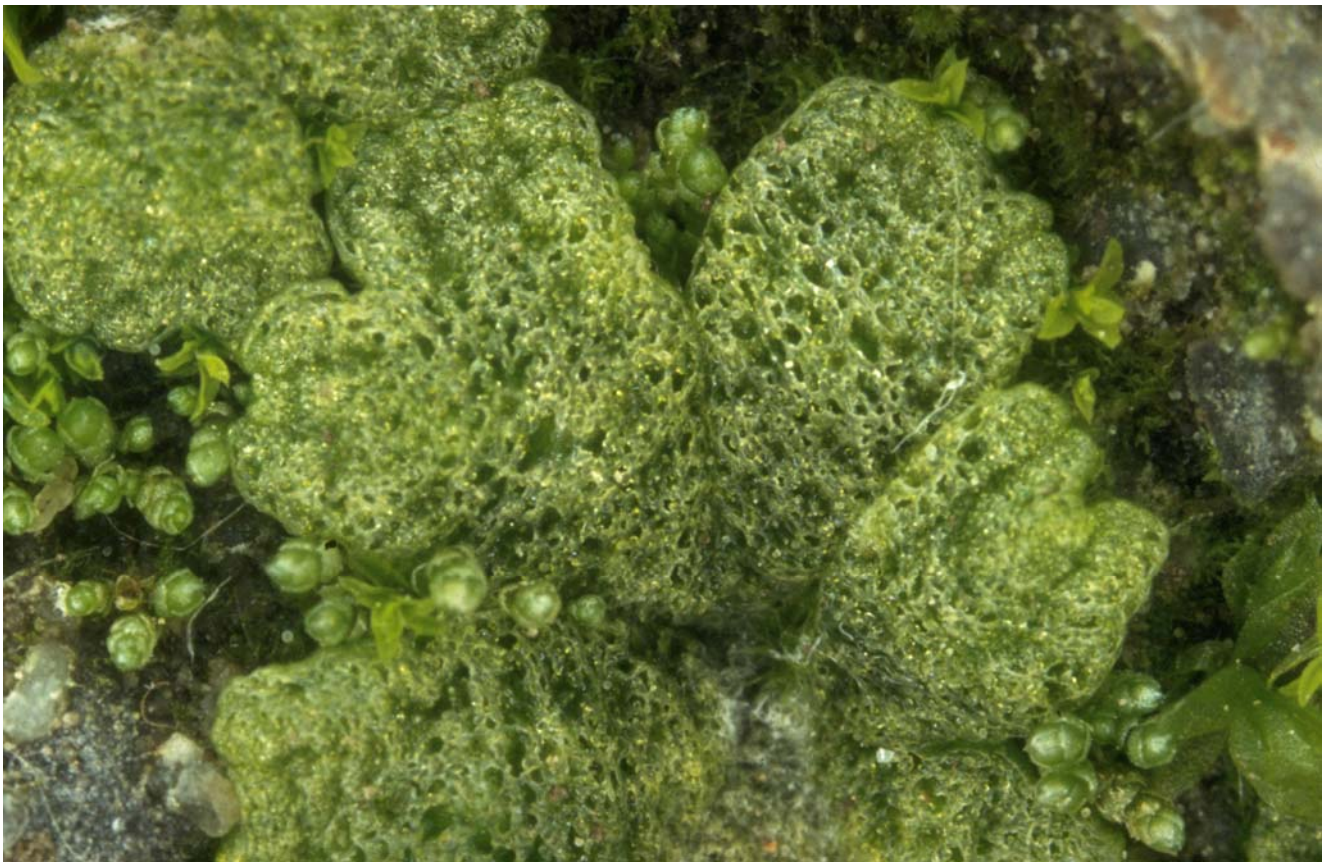

Figure 1. ***Riccia cavernosa***, a thallose liverwort that dries out during drought and recovers in the fall when rain returns. Photo by Jan-Peter Frahm, with permission.

Water Relations on Land

Proctor (2014) points out that one of the basic needs of bryophytes is that of coping with the intermittent availability of water. To this end, poikilohydry is efficient at the small scale of a bryophyte, whereas endohydry is more beneficial for the large tracheophytes.

Physiological adaptations relate on one end to the morphology and on the other to the biochemistry. Although we have recognized morphological characters for a very long time, few have actually been tested experimentally on a large scale for their adaptive value in altering physiology. The biochemical adaptations, on the other hand, constitute a new and emerging field of bryology, one that coincides closely with physiology of tracheophytes. By using the more easily studied bryophytes, we have gained the possibility of better understanding of the physiology of tracheophytes. This unusual interest in bryophytes is largely because of the relative ease with which genes can be moved into them or knocked out of them and their expressions be observed. And both bryophyte and fern gametophytes exhibit desiccation tolerance, whereas this ability is rare among sporophytic seed plants (Watkins *et al*. 2007). Long live the gametophytes! Even the lichens seem to have less desiccation tolerance than the bryophytes (Green *et al*. 2011).

Oliver *et al*. (2000) hypothesized that for photosynthetic plants to move onto land, desiccation tolerance was crucial. Using species of "resurrection plants" from both bryophytes and tracheophytes, Fisher (2008) concluded that desiccation tolerance arose among propagules as a means of survival. In bryophytes, nearly every part is a potential propagule in most species. For example, Maheu (1902) found that the moss ***Tortula muralis*** (Figure 2) would regenerate protonemata after

being stored dry for 14 years. Physiological adaptations may permit the bryophyte to retain water or to recover from loss of water, and to change its strategies with the seasons or the climate.

Figure 2. ***Tortula muralis***, a moss species that can survive drought as protonemata. Photo by Christophe Quintin, through Creative Commons.

Alpert (2000) presented two main puzzles from the observed habitat patterns of desiccation-tolerant plants. "What are the mechanisms by which plants tolerate desiccation?" and "Why are desiccation-tolerant plants not more ecologically widespread?" There appear to be multiple mechanisms of tolerance, including protection from oxidants and loss of normal configuration of macromolecules during dehydration. Alpert suggests that their inability to occupy a wide ecological range is due to their inability to maintain a cumulative positive carbon balance during their repeated wet/dry cycles and the tradeoffs between desiccation tolerance and growth rate.

Drought Tolerance vs Avoidance

As clear as the two words **tolerance** and **avoidance** may seem, they can lead to confusion because of differences in perspective. During (1979) tells us that **drought tolerance** is the ability to survive and maintain activity despite a lack of water in the environment. Proctor (2000) gives a more physiological definition that considers drought-tolerant plants to be those that are able to maintain a more or less normal metabolism at lowered cell volume and water potential, while tolerating elevated ionic concentrations in the cytoplasm and external environment. This physiological type of maintenance may be in evidence for the drought-tolerant ***Hedwigia ciliata*** (living on exposed boulders; Figure 82) and ***Grimmia pulvinata*** (often living on concrete; Figure 3). During a 5-day sequence of natural field drying, they showed no sign of plants drying and both maintained their photochemical efficiency, exhibiting normal day-night patterns (Schroeter *et al*. 1999).

Plants that show **tolerance** have vegetative parts that endure the stress period as best as possible (During 1979). But where is that lack of water, in the environment, or in the plant? I prefer to clarify this and say that **drought tolerance** is the ability of the plant to survive in a **habitat** that becomes dry. **Desiccation tolerance** is the ability of the **plant** to survive periods during which the **cells** are water-stressed and the plant itself has become dry; it suffers dehydration of all its metabolic systems. Such vegetative desiccation tolerance is rare among tracheophytes, with few species withstanding vegetative desiccation: 60-70 species of fern and fern allies and 60 species of angiosperms (Oliver *et al*. 2000). Instead, most tracheophytes survive through reproductive structures. Bryophytes (and lichens), on the other hand, exhibit vegetative desiccation tolerance as well as through reproductive structures (Kappen & Valladares 1999; Proctor et al. 2007).

Figure 3. ***Grimmia pulvinata***, a drought tolerator growing on concrete. Photo with permission from Botany Department website, University of British Columbia, Canada, with permission.

For sake of clarity, let us consider **drought** to be a condition of the environment and **desiccation** to be a condition of the plant, in this case the bryophyte. For tracheophytes, drought in the environment nearly always causes desiccation in the plant, but for bryophytes, this may not so often be the case.

Using that terminology, **drought tolerance** can be accomplished in two ways: **desiccation tolerance** and **desiccation avoidance**. **Desiccation avoidance** is the ability to prevent desiccation from occurring within the plant or the ability to go into a **dormant stage** during periods of low water availability; it is often characterized by plants that die and leave stress-tolerant **diaspores** (any structures that become detached from parent plant and gives rise to new individuals) that will grow the next season. Note the use of the word **stage** here, not **state**. For bryophytes, spores and gemmae provide dormant **stages**, although the entire **mature** sporophyte might be considered a stage that does not require water. On the other hand, a desiccation-tolerant vegetative plant can go into a dormant **state**, where metabolic activity slows to an imperceptible level, but where this same plant stage will regain its ability to gain carbon and grow.

Using these concepts, Smith (1986) considers that true desiccation tolerance among plants is rare or non-existent. The tracheophytes may in fact never be desiccation tolerators (Larcher 1983), generally relying on avoidance by storing water or by going into a dormant life cycle stage until the return of sufficient water (Smith 1986). Bryophytes, on the other hand, can be true desiccation tolerators, and suffer relatively little damage at relative humidity levels far below those tolerated by tracheophytes (Table 1). They do this in a vegetative stage through mechanisms that avoid desiccation damage.

Desiccation resistance, the ability to maintain an adequate water supply under drought conditions, is actually **drought avoidance**. Drought avoidance also includes the

ability to revert to a dormant stage that requires no water, such as spores and tubers. Water is essential to all life, and the ability to obtain it under limiting conditions or to store it until more is available permits some organisms to live in conditions that are intolerable for others. Most perennial bryophytes do not have the option of disappearing into the soil for the winter, and in fact the period of greatest drought for many of them is in the summer. However, bryophyte growth generally ceases during this hot and often dry time and metabolic activity is slowed considerably, if not completely.

Table 1. Comparison of desiccating percent relative humidity levels tolerated by various groups of plants. Table modified from Larcher (1983).

Plant	%RH Tolerated without injury	%RH Moderate injury
Marine algae		
Deep water algae	99-97	14-41
Algae of the ebb line	95-86	69-204
Intertidal algae	86-83	204-252
Liverworts		
Hygrophytes	**usually 95-90**	**92-90**
Mesophytes	**usually 92-50**	**90-36**
Xerophytes	**usually (36)-0**	**0**
Mosses		
Water mosses and hygrophytes	**95-90**	**69-141**
Mesophytes	**usually 90-50 extreme 10**	
Xerophytes	**usually 5**	**0**
Fern gametophytes		
Forest ferns	>90	50-90
Rock ferns	40-60	20-30
Tracheophytes (tissue sections)		
Leaf epidermis		96-92
Mesophyll	96	95-90
Root cortex		97-95

Both desiccation avoidance and desiccation tolerance strategies are available to bryophytes (Figure 4-Figure 5). You will soon see that whereas desiccation tolerance may be unavailable to tracheophytes, it is of considerable importance for bryophytes.

Desiccation Tolerance

In 1702 Anthony von Leeuwenhoek examined dry sediment from a gutter after hydrating it for an hour, and found tiny animals swimming about (Alpert 1982, 2000). These animals, rotifers, seemingly had arisen from the dead. Leeuwenhoek followed with experiments that showed these animals could remain in this dry state for months. But he did not imagine that they had lost all moisture because they retained their normal oval shape. During the next century, experiments demonstrated that rotifers, nematodes, and tardigrades all could undergo a dry, dormant state. In fact, some organisms can survive for over ten years without water, reaching immeasurably low water potentials (Alpert 2000). In this desiccated state they can endure temperature extremes from 0272 to 100°C.

But what was this dormant state? Words such as **anabiosis**, **abiosis**, **revivification**, and **resuscitation**, arose to describe the dry state and ability to return from it (Alpert 1982). The term **cryptobiosis**, however, seems most appropriate, avoiding the question of whether or not the organism is still alive. Instead, it refers to the state of an organism when it shows no visible sign of life, when its metabolic activity is immeasurable (hidden life).

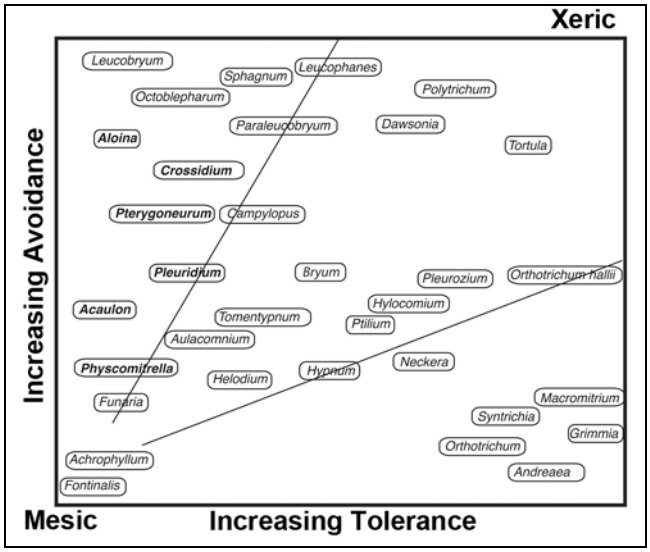

Figure 4. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

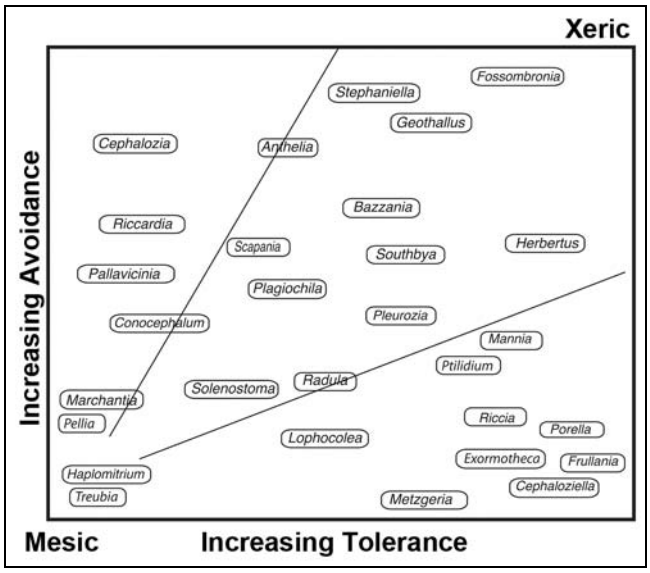

Figure 5. Distribution of a number of genera of mosses relative to mesic and xeric conditions and their strategies of avoidance vs tolerance. Modified from Vitt *et al.* 2014.

Low temperature physics helped to clarify the issue. Recognizing absolute zero as -273ºC, the temperature at which everything freezes and all molecular movement stops, Becquerel (1950a, b, c, 1951) subjected tardigrades, rotifers, algae, seeds, bacterial and fungal spores, fragments of the lichen *Xanthoria parietina*, and leaves of the mosses ***Grimmia*** (Figure 79-Figure 80) and ***Barbula*** (Figure 6) to two-hour treatments at temperatures very close to 0.0°K (0.05-0.008ºK). These organisms returned to their active state and bacteria even reproduced. ***Syntrichia ruralis*** (Figure 77-Figure 93) survived after 24 hours at -198°C

(Bewley 1973). Based on typical reduction in metabolism of ½ for every 10ºC drop in temperature, Becquerel calculated that at absolute zero metabolism would be 7.13 trillion times as slow as the normal rate at 15ºC (see Alpert 2000).

Figure 6. ***Barbula convoluta*** var. ***commutata***, a species that survives at temperatures close to 0°K. Photo by Michael Lüth, with permission.

This did not support the hypothesis that life ceased and then was reactivated. In fact, three arguments can be made against that hypothesis, some of which have been demonstrated for desiccated mosses. First, Dilks and Proctor (1976b) have demonstrated that mosses recover more slowly as duration of desiccation increases, ultimately reaching a duration from which they are unable to recover. Second, for most organisms in this cryptobiotic state, there is still a minute uptake of oxygen (Pigòn & Weglarska 1955a,b), indicating retention of metabolism. Third, there is a point at which all these organisms die.

Such desiccation tolerance, a common phenomenon among bryophytes, seems to have been lost in the evolution of tracheophytes. Rather, tracheophytes have experienced increased growth rates, more structural and morphological complexity, and mechanisms for conserving water rather than recovering from its loss (Oliver *et al*. 2000). Only in their reproductive structures, particularly seeds and underground storage organs, have tracheophytes retained and diversified the strategy of desiccation tolerance.

Norris (1990) contends that four dimensions of water relations must be understood to understand the problems of bryophytes compared to tracheophytes. To this I have added the fifth as a result of more recent experiments:

1. hydration/dehydration frequency
2. hydration duration
3. dehydration duration
4. degree of water loss
5. rate of water loss.

With the need for repair whenever moss cells become dry, it is not surprising that the frequency of the wet-dry cycle and the duration of the hydration period are important in determining survival. Even in such xerophytic bryophytes as ***Grimmia pulvinata*** (Figure 3), living on rock walls in Britain, the median length of wet and dry periods is generally between 5 and 15 hours (Proctor 2004). The longest dry periods in early summer are typically 15-17 days, with the longest continuously wet period lasting nearly 28 days. The moss cushions typically remain wet about 1.7 times the duration of rain. It appears that dew fall is insufficient to cause hydration in this species, perhaps because water drops are trapped by the long hairs instead of reaching the leaf lamina. Such a mechanism could protect the species against frequent (daily) wet-dry cycles in which the nightly wet period is insufficient for damage repair before the moss becomes dry again. Growth occurred primarily in autumn when the moss was wet for long periods, despite relatively low levels of irradiation.

Like others, Stark *et al.* (2013) argued that desiccation tolerance is the most important evolutionary innovation permitting plants to colonize land. They used the desert moss ***Pterygoneurum lamellatum*** (Figure 7) and chlorophyll fluorescence to test recovery from drying of 30 minutes to 53 hours. As in other studies, rate of drying is a major factor in recovery, with only the shoot apex escaping the severe damage of very rapid drying. Rapidly desiccated shoots have slower growth rates, fewer regenerative shoots, and a compromised photosynthetic system. The responses to differences in rate of drying indicate that this xerophytic moss has inducible desiccation tolerance, in contrast to the assumption that xerophytic bryophytes have only constitutive desiccation tolerance.

Figure 7. ***Pterygoneurum lamellatum***, a desert moss with inducible desiccation tolerance. Photo by Michael Lüth, with permission.

Although ***Sphagnum*** (Figure 63) may not be a good model for other kinds of bryophytes, it gives us an idea of the evaporative relationships of these non-tracheophytes. ***Sphagnum*** in a foggy coastal blanket bog in Newfoundland demonstrated that the bog surface loses little water during foggy periods, due, in part, to absence of a vapor pressure deficit. On the other hand, during dry, clear periods the surface of the bog dries, increasing the surface resistance to evaporation (Price 1991); at the same time, higher available energy from the sun causes the rate of evaporation to be higher than on foggy days. This results in a daily evaporation rate of 1.5 mm per day on clear days, contrasting to 0.7-1.1 mm per day for foggy or rainy days.

If we put the two strategies, avoidance and tolerance, into a different perspective, we find that some species tend to avoid drought by holding water more effectively while some survive better at a lower water content. Table 2 lists the survival time of a number of bryophytes. Mechanisms to accomplish survival vary. As we have seen already (in Chapter 7-4a & b of this volume; Li *et al*. 1992)

Sphagnum magellanicum (Figure 8) is superior to ***S. papillosum*** (Figure 9) at retaining water and transporting it from lower parts of its environment, but ***S. papillosum*** has a greater rate of survival (95%) after laboratory drying (80% for ***S. magellanicum***). Thus, ***S. magellanicum*** is more of a drought avoider whereas ***S. papillosum*** is more of a short-term drought tolerator. On the other hand, ***S. papillosum*** death (65%) surpasses that of ***S. magellanicum*** (50%) when both are dried for 30 days.

Figure 8. ***Sphagnum magellanicum***, a moss with good water retention and transport but inferior desiccation survival. Photo by Michael Lüth, with permission.

Figure 9. ***Sphagnum papillosum***, a moss with poor transport and water holding ability, but good desiccation survival. Photo by Michael Lüth, with permission.

Table 2. Known durations of desiccation survival in bryophyte gametophyte plants.

Sphagnum fuscum	2-4 d	Schipperges & Rydin 1998
Sphagnum papillosum	2-4 d	Schipperges & Rydin 1998
Sphagnum balticum	2-4 d	Schipperges & Rydin 1998
Sphagnum cuspidatum	2-4 d	Schipperges & Rydin 1998
Sphagnum magellanicum	2-4 d	Schipperges & Rydin 1998
Sphagnum magellanicum	14 d	Sagot & Rochefort 1996
Sphagnum fallax	14 d	Sagot & Rochefort 1996
Fontinalis flaccida	3 mos	Glime unpubl
Barbula torquata	18 mos	Moore *et al*. 1982
Oxymitra	4 yrs	Volk 1984
Riccia canescens	7 yrs	Volk 1984
Grimmia laevigata	10 yrs	Breuil-Sée 1993
Syntrichia ruralis	14 yrs	Breuil-Sée1993
Tortula muralis protonema	14 yrs	Maheu 1902
Anoectangium compactum	19 yrs	Malta 1921
Riccia macrocarpa	23 yrs	Breuil-Sée1993

Lloyd Stark (pers. comm. 18 July 2015) found conflicting results among the publications on the duration of the dry period of ***Sphagnum***. Desiccation tolerance alone did not explain the conflicting results. Sagot and Rochefort (1996) dried fragments three species of ***Sphagnum*** [***S. fallax*** (Figure 14-Figure 16), ***S. fuscum*** (Figure 10), ***S. magellanicum*** (Figure 8)] and dried them at 60% relative humidity. These species were able to tolerate up to 14 days of desiccation under these conditions. On the other hand, when Schipperges and Rydin (1998) completely dried ***S. fuscum*** and ***S. magellanicum***, and three other species, none of the five species survived. On the other hand, if the water content was maintained above 100% (normal hydration of ***Sphagnum*** is much greater than that), all the species survived 3-12 days in this "dry" condition. But with the standard water content considered to be near 10% dry weight (~equilibration with 50% relative humidity), This hardly qualifies as dry.

Hájek and Beckett (2008) likewise found that hummock species ***Sphagnum magellanicum*** (Figure 8) and ***S. fuscum*** (Figure 10) under desiccation conditions lose more water before turgor starts dropping than do other ***Sphagna*** from less exposed habitats (73% vs 56% on average). Nevertheless, the osmotic potentials at full turgor are similar in all species (-1.1 MPa). Unlike the desiccation-tolerant ***Racomitrium lanuginosum*** (Figure 78) and ***Syntrichia ruralis*** var. ***arenicola*** (Figure 77), the hummock ***Sphagnum*** species have more rigid cell walls than those of wet habitats. Thus, the leaves of hummock species lose turgor at higher relative water contents (0.61) than species lower in the hummock-hollow complex (0.46). Hummock species also begin a photosynthetic decline sooner during drying. On the other hand, the hummock species recover more completely after rehydration.

Hajek and Vicherova (2014) were able to harden 13 species of ***Sphagnum*** (Figure 8-Figure 9) to desiccation. Hardening agents included drought, slow drying, ABA application, and chilling or frost. They measured tolerance by recovery of chlorophyll fluorescence parameters after severe desiccation. The hardening was accomplished by subjecting the shoot apices to a very high relative humidity (98-99%) for seven days prior to exposing them to desiccating conditions. With that preparation, the bryophytes were able to tolerate 56% relative humidity. This indicates that in ***Sphagnum*** desiccation tolerance is inducible.

Despite its ability to induce desiccation tolerance, one important role of ***Sphagnum*** (Figure 8-Figure 9) as an ecosystem engineer is its ability to retain water (Hajek & Vicherova 2014). Its ability to survive desiccation is seasonal. Following initial dehardening in the lab, untreated shoots of ***Sphagnum*** lack desiccation tolerance. Nevertheless, desiccation tolerance was induced by all hardening treatments except chilling, and especially by slow drying, even in the aquatic section *Cuspidata*. Under field conditions, ***Sphagnum*** species in hollows and lawns developed desiccation tolerance several times during the growing season as the precipitation and lowered water table created changing conditions. On the other hand, hummock and aquatic species responded only to frost in late autumn, becoming desiccation tolerant. The protonemata did not develop desiccation tolerance, suggesting that this may be a limiting stage in the life cycle. The desiccation avoiders do

not develop desiccation tolerance and must live in compact hummocks or submerged. Thus, there seems to be a tradeoff between desiccation tolerance in species lower on the hummocks and submerged vs resources spent on water retention and desiccation avoidance at higher positions.

Figure 10. ***Sphagnum fuscum***, a hummock species. Photo by Michael Lüth, with permission.

Hájek and Beckett (2008) suggest that the higher water-holding capacity of hummock ***Sphagna*** (Figure 8-Figure 10) would allow them to continue their metabolism longer during desiccation, *i.e.*, they have greater desiccation avoidance. On the other hand, their faster recovery makes them desiccation tolerators. Species in lower positions suffer fewer wet-dry cycles but have more elastic cell walls, permitting them to maintain turgor through a wider range of conditions and thus continue metabolism.

Hájek and Beckett (2008) found that ***Atrichum androgynum*** (Figure 11), a moss of the New Zealand forest floor, behaved in a manner similar to hummock ***Sphagnum*** (Figure 8-Figure 10) species. Proctor (2000) suggests that it is the ability to use external water conduction that permits bryophyte leaf cells to maintain full turgor most of the time. Their carbohydrate content is similar to that of embryos in desiccation-tolerant seeds. They are furthermore able to recover rapidly without protein synthesis. As larger plants evolved, vegetative desiccation tolerance was lost; growth rates increased, structural and morphological complexity evolved (Oliver *et al*. 2000), and water conservation mechanisms were selected over rapid intake and recovery.

Oliver *et al*. (1993) noted that carbon balance, damage limitation, and cellular repair are necessary components of desiccation tolerance. Using desiccation tolerance of three desiccation-tolerant species of ***Syntrichia*** (Figure 12-Figure 13, Figure 77), they learned that electrolyte leakage is not an important measure of tolerance, but that differences in protein synthesis could be used to assess damage limitation. Using this assessment, they found the order of tolerance in descending order to be ***Syntrichia caninervis*** (Figure 12), ***S. ruralis*** (Figure 77), and ***S. norvegica*** (Figure 13). This basis of classification and ranking correlates well with the water stress considered to be present in their natural habitat.

Figure 11. ***Atrichum androgynum***, a species that retains turgor at lower water concentrations, much like a hummock ***Sphagnum*** species. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 12. ***Syntrichia caninervis***, the most desiccation-tolerant of three ***Syntrichia*** species on the basis of protein synthesis. Photo by Michael Lüth, with permission.

Wagner and Titus (1984) compared two ***Sphagnum*** species – ***S. fallax*** (Figure 14-Figure 16), a hollow species that lives close to the water table, and ***S. capillifolium*** (Figure 17-Figure 18) (=***Sphagnum nemoreum***), a hummock species. Here, the relationship is somewhat surprising. The hollow species ***S. fallax*** is more desiccation tolerant than the hummock dweller ***S. capillifolium***. ***Sphagnum fallax*** not only recovers a greater proportion of its predesiccation photosynthetic rate, but it also has a higher survival rate after 5-10 days of desiccation. This relationship can be explained by events in its habitat. ***Sphagnum fallax*** dries more frequently and for longer periods of time than does the hummock-dwelling ***S. capillifolium***. ***Sphagnum capillifolium*** is able to retain moisture longer in the field. Growth habit may explain this ability, with ***S. fallax*** being larger and having a wide-spreading head, whereas ***S. capillifolium*** has a compact capitulum (head) (Figure 18) and lives in tightly packed clumps (Figure 17).

Figure 13. ***Syntrichia norvegica***, the least desiccation-tolerant of three ***Syntrichia*** species on the basis of protein synthesis. Photo by Michael Lüth, with permission.

Figure 14. Habitat of ***Sphagnum fallax*** on hummocks in the pool where they undergo water level fluctuations. Photo by Michael Lüth, with permission.

Figure 15. ***Sphagnum fallax*** showing spreading branches in capitula and large spaces between plants. Photo by Michael Lüth, with permission.

Figure 16. Close-up view of a hummock of ***Sphagnum fallax***. Photo by Michael Lüth, with permission.

Figure 17. ***Sphagnum capillifolium capillifolium*** hummock showing the tight relationship between plants. Photo by Barry Stewart, with permission.

Figure 18. ***Sphagnum capillifolium*** capitulum showing the tightness of the branches. Photo by Bernd Haynold through Creative Commons, with permission.

Bu *et al*. (2013) consider that peatlands have hummocks with drought-tolerant species and hollows with drought-intolerant species. They found that drought reduces the biomass production, height increment, and side shoot production of both hummock species [***Sphagnum palustre*** (Figure 19) and ***S. capillifolium*** (Figure 17-Figure

18)] and hollow species [***S. fallax*** (Figure 14-Figure 15). Bu and coworkers found that the leaf hyaline cell percentage increases in the hummock species but not in the hollow species. Furthermore, the nitrogen and carbon contents of the hummock species respond more to drought than they do in the hollow species. Instead, it is the presence of neighboring species of ***Sphagnum*** that causes the decrease in carbon in all three species. Despite this effect, there is no change in the competition under wet or dry treatment for any of the six species combinations. Contrary to expectations, ***Sphagnum fallax*** exhibits a change from facilitation in wet conditions to competition under dry conditions. This suggests that hummock species can facilitate the hollow species in wet environments but can outcompete them for water under drying conditions. The inability of hollow species to grow on hummocks could be the combination of superior competitors and the greater drought.

Figure 19. ***Sphagnum palustre***, a drought-tolerant hummock species. Photo by Michael Lüth, with permission.

Wood (2007) summarized vegetative desiccation tolerance of bryophytes. Defining it as the "unique ability to revive from the air-dried state," he considered desiccation-tolerant species to be those that can survive equilibration with either modestly dry air (*i.e*., 70-80% RH) or extremely dry air (*i.e*., 0-30% RH). He considered these desiccation-tolerant species to comprise seven bryological classes: **Andreaeopsida**, **Bryopsida**, **Polytrichopsida**, and **Tetraphidopsida** (mosses), **Jungermanniopsida** and **Marchantiopsida** (liverworts), and the **Anthocerotopsida**. This omits the **Andreaeobryopsida** and the **Sphagnopsida**. The **Andreaeobryopsida** may be omitted simply due to lack of data. The **Sphagnopsida**, on the other hand, do indeed have desiccation tolerance in at least some species. In defense of the omissions, only 210 out of ~21,000 bryophyte species (*ca*. 1.0%) have been experimentally determined to possess vegetative desiccation tolerance – 158 species of mosses, 51 species of liverworts, and 1 species of hornwort.

Desiccation Avoidance

Many options of desiccation avoidance are available to tracheophytes that are not available to bryophytes. Bryophytes cannot make use of deep roots or increase the length of their roots (or in bryophytes - rhizoids), as do many tracheophytes, because this would have little effect at the scale of a bryophyte. Nor do they have large underground storage organs to permit dormancy. But many do have underground **tubers** (see Chapter 4-10 of this volume) that store significant quantities of lipids or starches (Duckett & Pressel 2003) and that seem to be an adaptation to drought avoidance (El-Saadawi & Zanaty 1990).

Bryophytes cannot conserve water by using an alternate photosynthetic pathway to store CO_2 (Rundel *et al*. 1979, James 1981) because it would provide no water conservation advantage due to their lack of leaf stomata. Their developmental structure does not permit the loss of leaves because no buds occur at the base of each leaf, and one must wonder if such a small stem could store sufficient energy to support the growth of new leaves prior to any new input from photosynthesis.

The plants protect each other from desiccation and may hide buds of younger shoots within the clump. In ***Bazzania trilobata*** (Figure 20), field plants are able to tolerate drying, whereas lab drying is lethal (Sollows *et al.* 2001). Field conditions do not provide the desiccation level one might suppose by measuring air moisture. But it is also likely that the drying rate is different, and the integrity of the clump may have been altered in the lab.

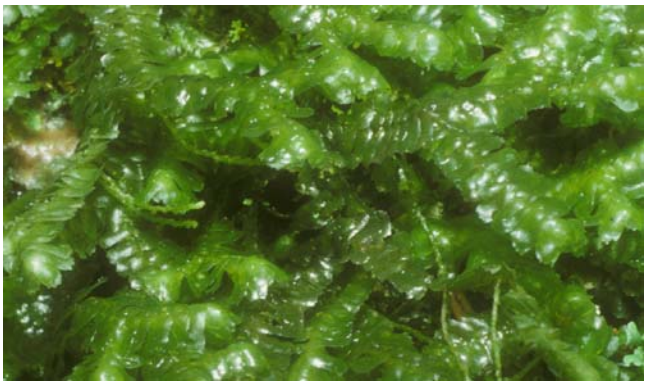

Figure 20. ***Bazzania trilobata*** illustrating overlapping leaves and layering of branches. Photo by Janice Glime.

Many bryophytes can roll their leaves, as do some vascular plants, and they have several other related options to reduce the exposed surface area. These include curling and contorting the leaves (see Chapter 7-4 in this volume), a mechanism that creates small air spaces and presumably decreases air movement across the leaf surface. Others appress their leaves closely to the stem, protecting the upper surface from exposure and overlapping leaves sufficiently to protect even portions of the back surface of the leaf from exposure. And, despite their lack of specialized energy-storing organs (with some exceptions), they do have life cycle options. Perhaps the most important of these adaptations is the ability to withdraw water from the cell and form extracellular ice, with desiccation tolerance being an important adaptation (Dilks & Proctor 1975). (See Chapter 7-9 and 7-10 for further information on effects of freezing.)

Life Cycle and Life Strategy Adaptations

Hedderson and Longton (1996) evaluated the relationship between life history traits and taxonomic group, relating these to water relationships. They found

that 40-50% of the life history variation was related to water relations. The capacity for water uptake and retention arranges species from short-lived **monoicous** (having both sexes on same plant) taxa that produce few, large spores to those **dioicous** (having separate sexes) taxa with the opposite traits. The **endo-ectohydric** (internal vs external water control) gradient similarly relates to the investment in spores as a function of life expectancy.

One way to survive dry periods is to avoid them by leaving your spores behind to carry on the species. In the Murray River Valley, Australia, where flooding occurs every spring, long dry periods ensue and many taxa such as the ephemeral mosses persist there as spores (Peintinger 1988). In such genera as ***Riccia*** (Figure 1), which typically inhabit seasonally dry areas, dispersal of spores by animals, aided by the ornamentation of the spore, is important (Volk 1984; see Chapter 4-8 in this volume). Survival is facilitated by the ability to endure temperatures as high as 80ºC when dry, whereas temperatures higher than 50ºC when wet will injure them.

Alternatively, ephemeral bryophytes such as ***Riccia cavernosa*** (Figure 1), ***Physcomitrella patens*** (Figure 21), and ***Physcomitrium eurystomum*** (Figure 22) are able to grow on the muddy floodplain soil (Peintinger 1988), then become dormant in the fall until water returns again.

Figure 21. ***Physcomitrella patens*** on wet soil after flooding recedes. Photo by Michael Lüth, with permission.

Figure 22. ***Physcomitrium eurystomum***, an ephemeral bryophyte that grows on floodplains. Photo by Michael Lüth, with permission.

For some bryophytes, altering their phenology according to available water is an adaptive strategy to take advantage of water when it is available. ***Octoblepharum albidum*** (Figure 23) in Nigeria produces antheridia and archegonia two months earlier when watered regularly (Egunyomi 1979). In nature, they produce archegonia during the rainy season, then produce capsules and take advantage of the dry season for dispersal of spores. This moss furthermore has leaves that can regenerate after as much as 29 weeks of dry storage, permitting an alternate means of propagation in those years when weather is not favorable for sexual fertilization.

In the very hot and dry summers of Kuwait, El-Saadawi and Zanaty (1990) found that a different avoidance strategy can be used. ***Bryum bicolor*** (Figure 24) forms subterranean rhizoidal **tubers** (see Figure 25) (Risse 1993) and stem tubers that permit it to be dormant as an avoidance mechanism, but it also exhibits tolerance in its protonemata, main stems, and stem apices (El-Saadawi & Zanaty 1990). ***Funaria hygrometrica*** (Figure 26) survives only by avoidance in the same conditions, using subterranean corm-like or bulbiform bases and bulbils to span the drought period.

Figure 23. ***Octoblepharum albidum*** growing epiphytically in India. This moss modifies its **phenology** (timing of life cycle events) when more water becomes available. Photo by Michael Lüth, with permission.

Figure 24. ***Bryum bicolor***, a moss that survives drought through stem apices and rhizoidal tubers. Photo by Michael Lüth, with permission.

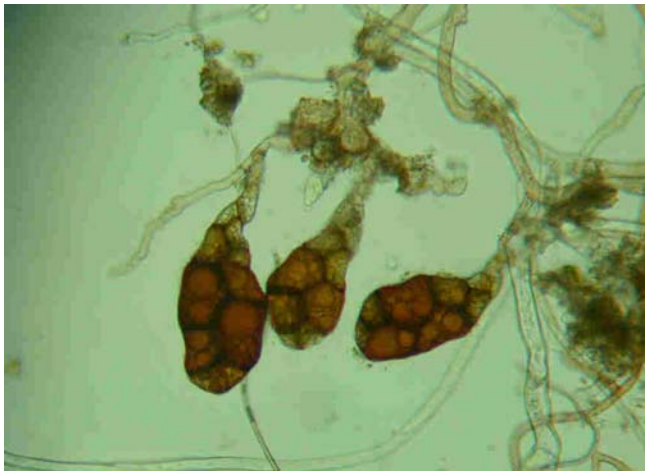

Figure 25. ***Bryum sauteri*** rhizoidal tubers, a means of surviving drought. Photo by David T. Holyoak, with permission.

Figure 26. ***Funaria hygrometrica*** with young sporophytes, growing abundantly on charcoal, where it will continue growth for several years until competition moves in. Note the bulbiform basal leaves that can protect the plant and young sporophyte during drought. Photo by Janice Glime.

Even in less xeric conditions, drought-resistant **tubers** (Figure 25) are present in such taxa as ***Atrichum tenellum*** (Figure 27), ***A. crispum*** (Figure 28) (Arts 1987), and ***Fissidens cristatus*** (Figure 29) (Arts 1986). In ***Haplodontium notarisii*** (Figure 31), tubers are viable for up to 10 years (Arts 1988).

Figure 27. ***Atrichum tenellum***, a moss that can survive drought as tubers. Photo by Michael Lüth, with permission.

Figure 28. ***Atrichum crispum***, a moss that can survive drought as tubers. Photo by Jan-Peter Frahm, with permission.

Figure 29. ***Fissidens cristatus***, a moss that is able to survive drought and freezing as tubers. Photo by Jan-Peter Frahm, with permission.

Some bryophytes actually require a dry season. In ***Orthotrichum anomalum*** (Figure 30), this dry period is necessary for the **operculum** (capsule lid) to dehisce (Johnsen 1969). The leafy gametophyte grows only when it is cool and moist, but watering during the dry period is detrimental.

Figure 30. ***Orthotrichum anomalum*** with dehisced capsules. Photo by Michael Lüth, with permission.

Seasonal Changes

As we have just seen, the physiological state of the bryophyte, and hence **desiccation tolerance**, varies with the **season**. Many bryophytes [*e.g.*, ***Plagiochila spinulosa***

(Figure 32), ***Hylocomium splendens*** (Figure 61-Figure 62), ***Scorpiurium circinatum*** (Figure 33), ***Syntrichia ruralis*** (Figure 93), ***Racomitrium aquaticum*** (Figure 34)] seem to be most sensitive during autumn and early winter, the times when most bryophytes resume growth after a hot summer (Dilks & Proctor 1976a). Desiccation tolerance increases from spring to a maximum in early summer, the season when many species become dormant. Some degree of acclimation may be occurring, resulting in increased tolerance as summer approaches (Richardson 1981).

Figure 31. ***Haplodontium notarisii*** with capsules, a moss that can survive for ten years as tubers. Photo by Jan-Peter Frahm, with permission.

Figure 32. ***Plagiochila spinulosa***, a leafy liverwort species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Figure 33. ***Scorpiurium circinatum***, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Figure 34. ***Racomitrium aquaticum***, a species that is most sensitive to desiccation during autumn and early winter. Photo by Michael Lüth, with permission.

Bryophytes apparently adjust their desiccation tolerance and resistance according to their experiences with the environment (Dilks & Proctor 1976a), as will be discussed in greater detail later with regard to rehydration. That is at least part of the reason for different studies showing different results, even from the same researchers. It is interesting that not all bryophytes adjust in the same way, with one group of bryophytes having their least desiccation tolerance time in autumn and winter and others in late summer in Britain (Figure 35), in this case coinciding with differences among their habitats. ***Andreaea rothii*** (Figure 36) seems to have no response to season.

Ochi (1952) examined the effects of season on drought tolerance and concluded that mosses with active buds at the beginning of the growing season are generally more drought resistant then than in other seasons. Seemingly in contrast to this statement, Ochi showed that in Japan ***Dicranum japonicum*** (Figure 37) survives drought longer (28 weeks) if the plant has active buds in early January rather than in early September or April (~4 weeks),

whereas ***Polytrichastrum formosum*** (=*Polytrichum attenuatum*; Figure 38), when dried on the same dates, survives longest when buds become active in September (>56 weeks compared to 28 in January and 11 in April). He concluded that these seasonal strategies represent three types of seasonal fluctuations in osmotic value: higher values in summer (dry season), lower in winter (wet season); higher in winter, lower in summer; no seasonal fluctuations (those from wet habitats).

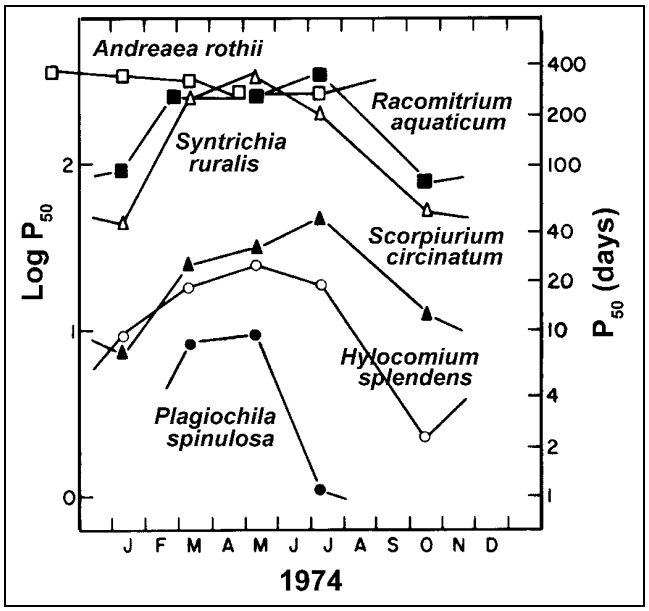

Figure 35. Relationship between season and maintenance of photosynthesis during desiccation of British bryophytes. P_{50} is the number of days (in this case) of desiccation at which photosynthesis upon rehydration is reduced to 50% its initial value. Redrawn from Dilks and Proctor (1976a).

Figure 36. ***Andreaea rothii***, a season-neutral moss with respect to its desiccation tolerance. Photo by Michael Lüth, with permission.

Davey (1997) found that in Antarctic bryophytes, the photosynthetic rate following a desiccation/rehydration cycle decreased from spring to summer to autumn. The pattern was clearest in the hydric taxa, with less effect in the xeric species.

Figure 37. ***Dicranum japonicum***, a moss where early January buds result in ability to survive drought longer. Photo by Li Zhang, with permission.

Figure 38. ***Polytrichastrum formosum***, a moss that survived longest when buds became active in September. Photo by David T. Holyoak, with permission.

Akande (1984, 1985) likewise attributed seasonal differences in desiccation tolerance of four **epiphytic** (growing on other plants, especially trees) bryophytes to changes in osmotic values, with osmotic values increasing from wet to dry season. He found that the mosses ***Entodontopsis nitens*** (=*Stereophyllum nitens*) and ***Calymperes palisotii*** (Figure 39) had a greater osmotic potential and greater desiccation tolerance than the leafy liverworts ***Mastigolejeunea florea*** and ***Frullania spongiosa***.

Figure 39. ***Calymperes palisotii***, a moss in which good osmotic potential increases desiccation tolerance. Photo by Scott Zona, with permission.

Physiological Adaptations

All of us have observed that bryophyte assemblages differ with habitats (*e.g.* Šinžar-Sekulić *et al*. 2005). Oliver *et al*. (2000) note that most of the desiccation-tolerant plants are bryophytes, in addition to algae and lichens. They agree that desiccation tolerance was an important step in the evolution of land plants. They suggested that such tolerance requires constitutive cellular protection coupled with active cellular repair. But as evolution progressed, plants gained structural and morphological complexity. Plants developed mechanisms that conserve water within the plant, and vegetative desiccation like that seen in bryophytes was no longer necessary.

But Alpert and Oechel (1985) contend that desiccation-tolerant plants are rarely present in the most xeric microhabitats, suggesting that in these locations they are unable to maintain a positive cumulative carbon balance. They demonstrated this in ***Grimmia laevigata*** (Figure 83), the dominant green plant on exposed granitic boulders in the California, USA, chaparral by measuring the response of net CO_2 flux to light, temperature, plant water content, and previous desiccation.

Among desiccation-tolerant bryophytes, rehydration is rapid, with leaves returning to normal form in as little as 2 minutes and chloroplasts returning to normal conformation in 2-5 minutes in such desiccation-tolerant mosses as ***Syntrichia ruralis*** (Figure 77) (Tucker *et al*. 1975; Oliver & Bewley 1984). On the other hand, following rapid drying such intolerant species as ***Cratoneuron filicinum*** (Figure 40) still have misshapen organelles after 24 hours, and about half the cells of slow-dried plants still contain misshapen organelles (Oliver & Bewley 1984). In slow-dried plants respiration recovers, but it does not in rapid drying of desiccation-intolerant plants.

Charron and Quatrano (2009) considered two general mechanisms for survival in the xeric aerial environment. The descendants of the early land plants evolved specialized transport tissues while the bryophytes retained and perfected their co-equilibrium of their water content with that of their surroundings, relying on cellular processes to recover from damages due to water stress.

Figure 40. ***Cratoneuron filicinum***, a moss species intolerant of rapid drying. Photo by Ivanov, with permission.

Bates (1997) examined the effects of wet/dry cycles on the nutrient economy of two pleurocarpous mosses of different habitats – ***Brachythecium rutabulum*** (Figure 56-Figure 57; wet ground, among grasses, logs; shade or open) and ***Pseudoscleropodium purum*** (Figure 41; grasslands and heaths). When provided with weekly drying periods of 24 hours every week, these plants had noticeably less biomass production than those plants that were continuously hydrated. ***Brachythecium rutabulum*** experienced bleaching of green tissues, unlike ***Pseudoscleropodium purum***. When NPK (mix of nitrogen, phosphorus, and potassium salts) was added to the growing solutions once a week, ***Pseudoscleropodium purum*** exhibited growth stimulation even among the weekly desiccated plants. Uptake of N was similar in both hydrated and desiccated plants of both species. P and K^+ were considerable in ***B. rutabulum***, but in desiccated plants they was greatly reduced. As with phosphorus, uptake of P and K^+ differed little between hydrated and intermittently desiccated ***Pseudoscleropodium purum***. In both species, P and K^+ were leaked from cells during desiccation, were retained on the cells by cation exchange, and taken up again during rehydration. But even this maintenance has a cost. K^+ and Mg^{+2} intracellular levels in new growth are maintained at the expense of exchangeable cations. Uptake is greatest during the early stages of recovery, most likely due to damaged membranes, and that is when the NPK application has the greatest effect on growth. These experiments suggest that ***P. purum*** has a lower nutrient requirement than ***B. rutabulum*** and they explain why ***B. rutabulum*** requires a more continuous hydration to maintain its greater production. An interesting revelation is the ability of these species to initiate new growth without additional nutrient absorption.

Bohnert (2000) asked what makes desiccation tolerable. He considered that bryophytes tolerated rapid desiccation, using protective mechanisms. Most research has focussed on repair mechanisms. The photosynthetic apparatus and cell integrity are maintained during desiccation, but rehydration leads to cellular damage. Despite this damage, recovery is rapid. **mRNA** (messenger RNA, the molecule that carries information from DNA to the ribosome) exists in **RNPs** (nucleoproteins that contain RNA) before the stress conditions arise. During recovery,

non-reducing sugars, **dehydrins** (group of proteins produced in response to cold and drought stress), and **rehydrins** (transcripts used during rehydration) appear. Hoekstra (2005) reported on the importance of fatty acid saturation in membranes in imparting survival of desiccation.

Figure 41. ***Pseudoscleropodium purum***, a species in which intermittent desiccation seems to have little effect on K and P uptake. Photo from Proyecto Musgo, through Creative Commons.

Yang *et al*. (2012) sought the genetic determinant(s) for stress tolerance. Using ***Syntrichia caninervis*** (Figure 12) they identified ScALDH21, a gene that responds to **ABA** (abscisic acid, a stress hormone; see Chapter 7-7 Water Relations – Biochemistry) and desiccation and that plays an important role in response to desiccation and salinity stresses.

When the desiccation-tolerant ***Syntrichia ruralis*** (Figure 77) is desiccated, it retains all its pigments, chlorophyll included, and is able to recover physiological function rapidly upon rehydration (Hamerlynck *et al.* 2002). But all is not equal among these plants of both sun and shade habitats. ***Syntrichia ruralis*** has lower plant mass, as well as lower tissue N, C, total photosynthetic pigment concentrations, and carbon isotope discrimination (Δ) values compared to shade plants. The ratio of carotenoid to chlorophyll in sun plants is typical of high light plants, but the ratio of chlorophyll *a* to chlorophyll *b* in these plants is lower than expected, resembling those of plants adapted to shade. As a consequence, the levels of optimal quantum efficiency of **PS II** ($\mathbf{F_v/F_m}$) (= variable fluorescence / maximum fluorescence; PS II is photosystem II of photosynthesis, where oxygen is liberated from water) are lower in the sun plants. Reciprocal transplants reveal that ***Syntrichia ruralis*** is able to adjust to altered light levels. This is evidenced by increases in F_v/F_m, **NPQ** (non-photochemical quenching), light-adapted PSII yield (φPS II) in transplanted sun plants, and concurrent decreases in sun-transplanted shade plants. Nevertheless, the transplanted sun plants did not adjust sufficiently to reach performance levels exhibited by the undisturbed shade plants. These plants demonstrate at least some ability to adjust to the loss of shade canopy or other disturbance in the light regime.

Sphagnum (Figure 8, Figure 9, Figure 14-Figure 18) has a unique cell structure (Figure 42) providing a water reservoir. We might expect that this reservoir increases the drying time, sparing the moss from the detrimental effects of rapid drying. But differences do exist among ***Sphagnum*** species.

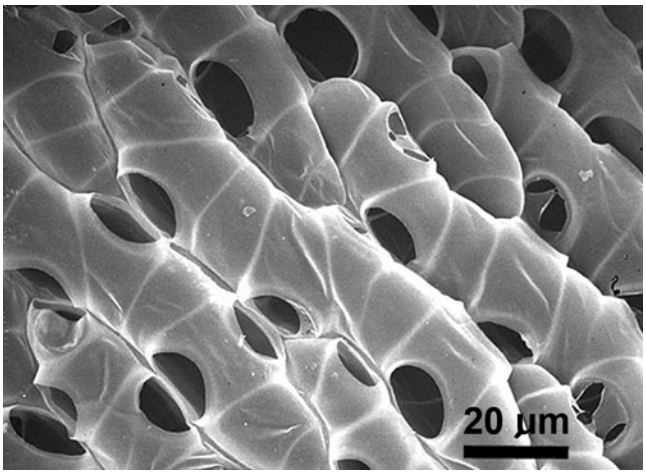

Figure 42. ***Sphagnum*** **hyaline leaf cells** and pores. Photo from Botany Department website, University of British Columbia, Canada, with permission.

In the hummock-forming ***Sphagnum fuscum*** (Figure 10) and ***S. magellanicum*** (Figure 8), desiccation results in a greater water loss before turgor sets in, compared to other non-hummock species (mean of 73% water loss vs 56%, respectively) (Hájek & Beckett 2008). The hummock species have more rigid cell walls than those of wet habitat species (epsilon = 3.55 vs 1.93 MPa, respectively). This rigidity results in loss of turgor in chlorophyllous cells at a higher relative water content in hummock species compared with species of wet habitats (0.61 vs 0.46) and at less negative osmotic potentials (-2.28 vs -3.00 MPa, respectively). Compared with other species, hummock ***Sphagnum*** (Figure 8, Figure 9) species that have been desiccated to -20 or -40 MPa recover more completely after rehydration. The **mesophytic** (intermediate habitat based on moisture) ***Atrichum androgynum*** (Figure 43) responds similarly to the hummock ***Sphagnum*** species.

Figure 43. ***Atrichum androgynum***, a moss that behaves similarly to hummock ***Sphagnum*** species when it loses water. Photo by Jan-Peter Frahm, with permission.

Under a given rate of desiccation, the hummock species of ***Sphagnum*** (Figure 8-Figure 10), with their higher water content, continue their metabolism longer than species with lower water-holding capacities (Hájek & Beckett 2008). And these species recover faster, indicating a higher drought tolerance. These behaviors permit them to survive in the drought-exposed hummocks. The species growing in wet habitats have smaller water-holding capacities but are able to maintain turgor and have more elastic cell walls that permit them to metabolize longer during drying.

Most ***Sphagnum*** (Figure 8-Figure 10) species live where intermittent desiccation is inevitable. Hence, this genus appears to have inducible desiccation tolerance (Hájek & Vicherová 2013). In experiments to **harden** (process by which a plant becomes tolerant to the effects of such stresses as frost and drought) the species, Hájek and Vicherová subjected them to slow drying, ABA application, and chilling or frost. In the laboratory, ***Sphagnum*** species that were de-hardened and remained untreated lacked desiccation tolerance. Slow drying, ABA application, and frost induced hardening and desiccation tolerance. The section ***Cuspidata*** (Figure 44) – aquatic species – did not exhibit hardening. Similar hardening occurs multiple times each year among hollow and lawn species in the field. Hummock and aquatic species, on the other hand, develop their tolerance only in late autumn, a phenomenon that Hájek and Vicherová attributed to frost. Protonemata, however, did not develop desiccation tolerance under any of the hardening treatments. The hummock species exhibit a tradeoff, having greater water-holding capacity to the detriment of their physiological desiccation tolerance.

Figure 44. ***Sphagnum cuspidatum***, an aquatic species that does not seem to experience hardening. Photo by Bernd Haynold, through Creative Commons.

Cratoneuron filicinum (Figure 40) demonstrates the effects of slow vs rapid drying on a semi-aquatic species (Krochko *et al*. 1978). In rapid drying, the cell contents are very disrupted and become increasingly disorganized over the next 24 hours. In slow drying, only some cells have this appearance while others maintain their cellular integrity. The greater the rate of drying, the more protein synthesis is reduced on rehydration, but it will resume following rapid water loss down to 50% of the fresh weight. On the other hand, respiration does not resume following rapid drying and rewetting.

Mode of Conduction

Can the mode of conduction provide a beneficial edge that permits success when faced with limited water? Raven (1999) claims there is a "mechanistically mysterious size limit" for poikilohydric, desiccation-tolerant plants, suggesting an upper limit of 1 m. Anderson and Bourdeau (1955) demonstrated that external water can travel only to a "certain level." Bowen (1933c) and Mankiewicz (1983, 1984a,b, 1987a,b) remind us that this upper limit is imposed by the height to which water can rise by capillarity alone, a distance Hébant (1977) considers to be only a few centimeters without the addition of other forces. As stated by Mankiewicz, "geometry of bryophytes may be constrained by the cohesive and adhesive forces of water," a statement he was able to confirm by empirical measures of flow rates through bryophyte colonies. However, we are reminded that most bryophytes receive their water from above, hence that capillary limit is of little importance for most of them. Therefore, we might ask, is the endohydric system important for the slow-growing, short bryophyte?

Bowen (1933a,b,c) compared conduction of bryophytes in wet, moist, and dry habitats. External water movement was faster than internal movement in all but two cases [***Thamnobryum alopecurum*** (Figure 50) and ***Plagiomnium undulatum*** (Figure 52)]. ***Plagiomnium undulatum*** has a well-developed internal conducting system and lacks significant capillary channels externally. ***Thamnobryum alopecurum***, on the other hand, typically lives where it is constantly wet from splashing or dripping water and seems to lack external conduction, perhaps due to external saturation. However, as the moisture of the habitat increases, the ability of the bryophyte plant to conduct decreases both externally and internally.

All of the taxa Bowen (1933a,b,c) studied had a **central strand** (Figure 45), varying considerably in relative size. But just how important is that strand in moving water from substrate to plant tissues? If the central strand is important in water movement, should we expect it to be most important in those mosses that suffer frequent drought conditions? In the epiphytic (but pleurocarpous) ***Hypnum cupressiforme*** var. ***filiforme*** (Figure 46-Figure 47), the central strand appears only occasionally and is absent in branches. In the boreal forest floor ***Rhytidiadelphus triquetrus*** (Figure 48), the cells are short with numerous transverse walls, suggesting inefficient water movement through walls. Nevertheless, in ***Aulacomnium palustre*** (Figure 49), internal conduction seems not to exist, despite a "relatively large central strand;" external conduction is rapid, suggesting that other factors, not the central strand, are more important in determining importance of internal versus external conduction.

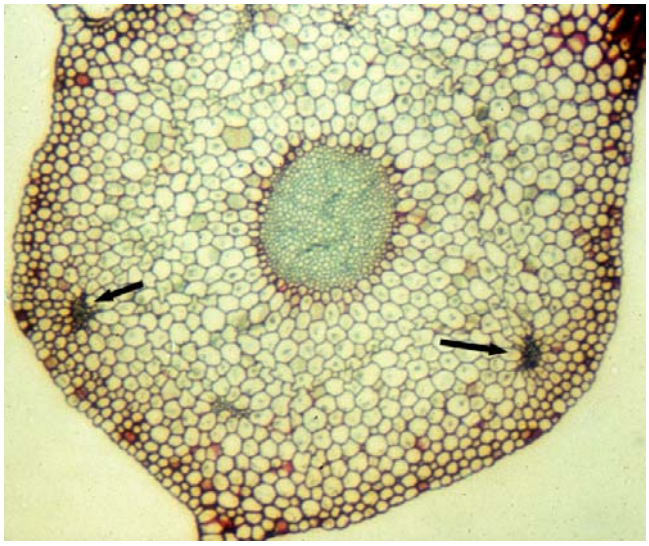

Figure 45. ***Mnium*** stem cross section showing central strand. Arrows indicate leaf traces. Photo by Janice Glime.

Figure 46. ***Hypnum cupressiforme*** in its epiphytic habitat. This moss usually lacks a central strand. Photo by Dick Haaksma, with permission.

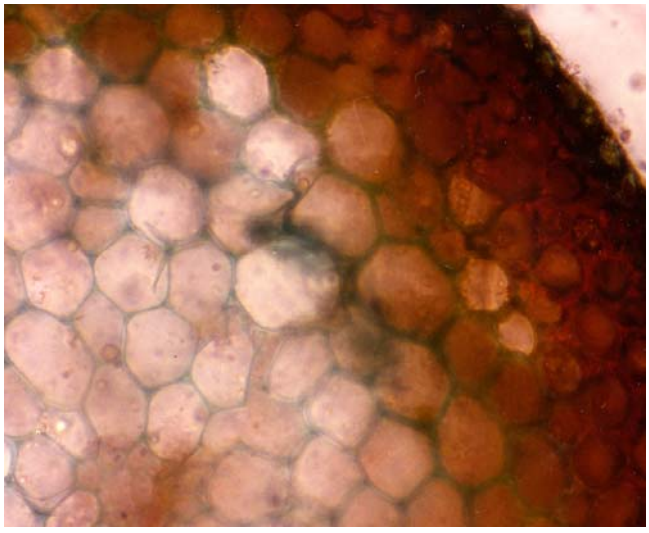

Figure 47. Cross section of stem of ***Hypnum*** sp. showing indistinct central strand. Photo by Isawo Kawai, with permission.

Figure 48. ***Rhytidiadelphus triquetrus*** on the forest floor. This moss has short stem cells with numerous transverse walls, making internal transport slow. Photo by Michael Lüth, with permission.

Figure 49. ***Aulacomnium palustre***, a moss with predominately external conduction despite its central strand. Photo by Janice Glime.

When Bowen (1933b) compared nine species of moist habitat bryophytes (Figure 53), she found that external conduction likewise predominated in all but ***Rhizomnium magnifolium*** (Figure 52; as ***Mnium punctatum***, but based on her description most likely what is now called ***Rhizomnium magnifolium***). ***Thamnobryum alopecurum*** (Figure 50), apparently erroneously reported in cm instead of mm in her table, has almost no water movement internally or externally (Mägdefrau 1935), but relies instead on the constant humidity of waterfalls and streamsides. Among the dry habitat mosses in the study, only ***Plagiomnium undulatum*** (Figure 52) exhibits more rapid internal conduction than external conduction.

Figure 50. ***Thamnobryum alopecurum***, a moss of dripping habitats that seems to have little water movement internally or externally. Photo by Michael Lüth, with permission.

Based on Bowen's (1931, 1933a,b,c) comparisons, we can derive little satisfaction about the relationship between the central strand and habitat. None of the species lacking a central strand were examined, nor were any extremely xerophytic or aquatic mosses or any liverworts examined. However, external adaptations to movement of water do seem to correlate with habitat, with those mosses from wet habitats having poor conduction capability both internally and externally, relative to taxa from drier habitats (Figure 53). The central strand appears to have only a minor role in conduction, being most useful in those taxa with a well-developed central strand, such as the **Mniaceae** (Bowen 1933c), and providing almost no value in those taxa with a small strand (Mägdefrau 1935; Zacherl 1956).

Despite Bowen's (1931, 1933a,b,c) small sample size and the presentation of "representative" data rather than means, one can still infer several patterns that indicate water pathway adaptations. The **Mniaceae** are a good example (Figure 52). There is good external conduction in ***Mnium hornum*** (Figure 52), where the leaf insertion is relatively small, but the leaves are strongly overlapping, as are the plants. In the very tomentose ***Rhizomnium magnifolium*** (Figure 52), with somewhat overlapping and encircling leaves, external conduction is relatively good, but internal conduction is much better than in ***Mnium hornum***. However, in ***Plagiomnium undulatum*** (Figure 52), where the leaves are non-overlapping and the leaf tapers to the equivalent of a petiole at insertion, external conduction is almost non-existent. It is noteworthy that members of this family are particularly difficult to rehydrate for slide preparation, presumably due to thickened cell walls and cuticular substances on the leaves. It is reasonable to expect rapid internal conduction in the **Mniaceae** because these mosses have well developed central strands of conducting tissue. In ***Plagiomnium undulatum*** the central strand occupies up to 2/3 of the stem diameter. Members of the family **Mniaceae** and ***Polytrichum commune*** (Figure 54-Figure 55) are also the only ones examined that have hydroids in the leaves (Bowen 1931, 1933a,b,c). As noted in ***Aulacomnium palustre*** (Figure 49), factors other than the size and construction of the central strand are important in determining relative conductance.

In ***Brachythecium rutabulum*** (or ***B. rivulare***?) (Figure 56-Figure 57), the slightly decurrent leaf bases form channels that retain capillary films of water. In ***Entodon rubicundus*** and ***Calliergonella cuspidata*** (Figure 58), internal conduction is appreciable in young tissues, becoming negligible in older stems (Mizushima 1980). Bowen (1933b) attributes this to the changes in **hypodermal tissues**, which are thin-walled in young stems, becoming thick-walled in older ones. Rather, the epidermis absorbs water and sends it cell-to-cell to the tip of the plant where the young hypodermal cells permit the water to penetrate to the center of the plant where a very thin central strand occupying about 10% of the stem exists. Entry of water into the apex is rapid, as is the external movement to the tip. ***Campylopus brevipilus*** (Figure 59) has a central strand of 5-15 cells in diameter. As might be expected in a genus so well adapted to dry habitats, even this more wetland species has little absorption through its stem epidermis and movement of water through the hypodermis is slow, entering primarily at the stem apex. Likewise, little conduction occurs from the base through the central strand.

Figure 51. ***Entodon rubicundus*** with capsules & dew drops, a species with internal conduction in young tissues. Photo by Shu Suehiro, permission pending.

Figure 52. Comparison of external morphology of three members of the Mniaceae. **Left:** ***Rhizomnium magnifolium***. **Middle:** ***Mnium hornum***. **Right:** ***Plagiomnium undulatum***. Photos by Michael Lüth, with permission.

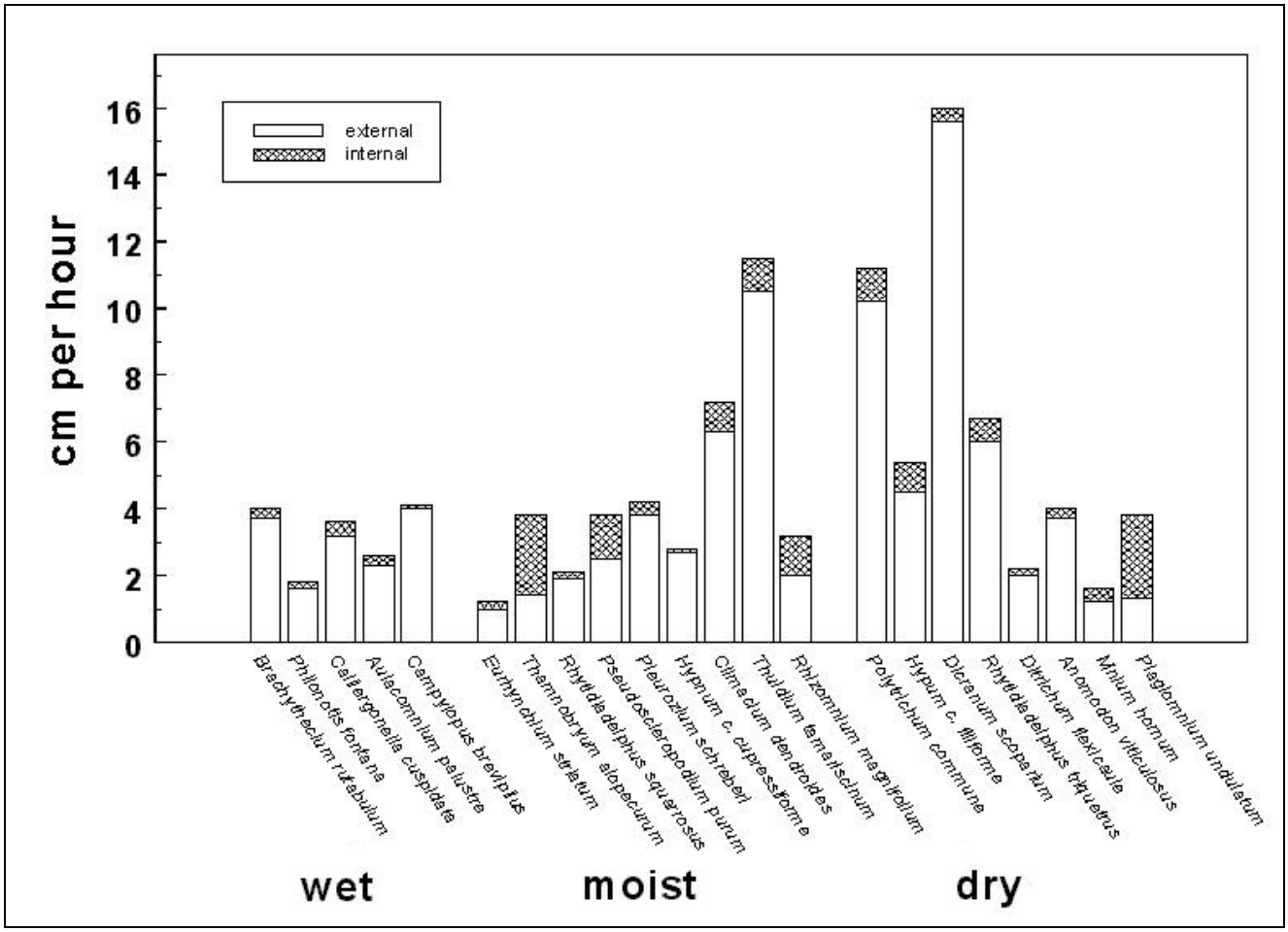

Figure 53. Comparison of movement of water up the stems in wet, moist, and dry habitat mosses. Note that for ***Brachythecium rutabulum***, ***Hypnum cupressiforme*** var. ***filiforme***, and ***Rhytidiadelphus triquetrus*** the internal movement is for 18 hours. (Based on the description of decurrent leaf bases and habitat, ***Brachythecium rutabulum*** may actually have been ***B. rivulare***.) For ***Thuidium tamariscinum***, ***Hypnum cupressiforme*** var. ***filiforme***, and ***Dicranum scoparium***, the external water reached the tip before one hour. In ***Ditrichum flexicaule*** and ***Anomodon viticulosus*** the water reached the tip in 15 minutes. Based on Bowen (1931, 1933a,b,c).

Figure 54. ***Polytrichum commune***, a moss with good internal conduction in stem and leaves. Photo by Michael Lüth, with permission.

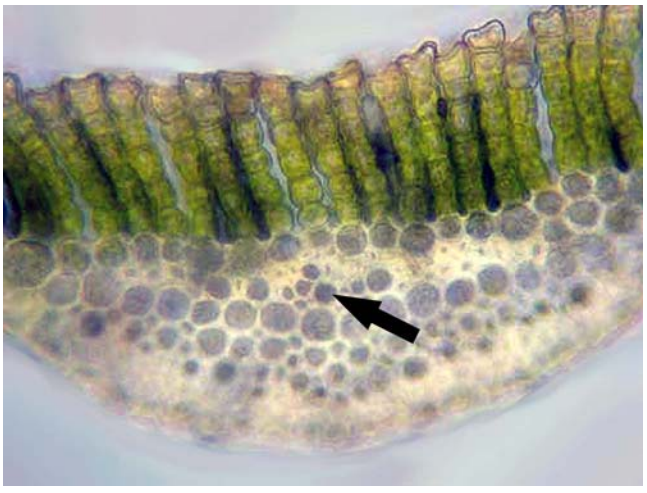

Figure 55. ***Polytrichum commune*** leaf cross section showing hydroids (**arrow**). Photo from Botany website, University of British Columbia, with permission.

Figure 56. ***Brachythecium rutabulum***, a moss whose leaf bases create capillary channels. Photo by Janice Glime.

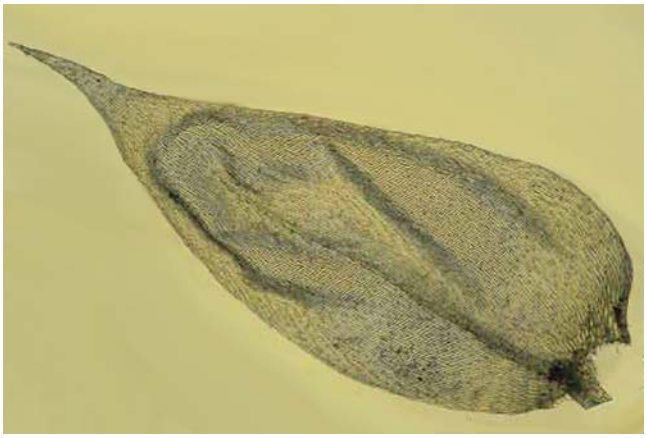

Figure 57. ***Brachythecium rutabulum*** leaf showing slight decurrency that aids in holding capillary water. Photo by Tom Thekathyil, with permission.

Figure 58. ***Calliergonella cuspidata*** has mostly internal conduction in young stems but lose it in older stems. Photo by Des Callaghan, with permission.

Figure 59. ***Campylopus brevipilus***, a moss in which water enters through the stem apex. Photo by Michael Lüth, with permission.

Could it be that the central strand serves a different function? In an Alaskan black spruce forest, Skré *et al.* (1983) found that endohydric ***Polytrichum commune*** (Figure 54-Figure 55), which has a well-developed central strand (Figure 60) and considerable internal conduction, suffers less moisture stress than the three ectohydric mosses studied [***Hylocomium splendens*** (Figure 61-Figure 62), ***Pleurozium schreberi*** (Figure 64), and ***Sphagnum subsecundum*** (Figure 63)] during the summer dry period. ***Hylocomium splendens*** remained below its water compensation point for nearly 50% of the July measurement period. The rates of water loss and moisture level required to reach field capacity correlate well with the moisture status observed for mosses in the field. This water retention in the endohydric ***Polytrichum*** supports the suggestion of Skré and coworkers that a major function of the central strand may be water storage.

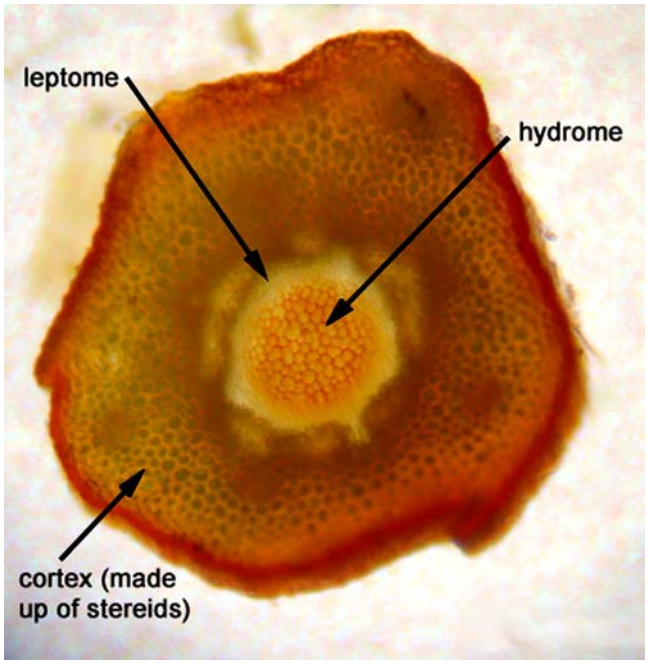

Figure 60. ***Polytrichum commune*** stem cross section showing hydrome. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 61. ***Hylocomium splendens***, an ectohydric, on black spruce forest floor. Photo by Janice Glime.

Figure 62. ***Hylocomium splendens*** stem cross section showing absence of central strand. Conduction is external. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 63. ***Sphagnum subsecundum***, an ectohydric moss. Photo by Michael Lüth, with permission.

Osmotic Potential and Turgor

Unlike tracheophytes, whose net photosynthesis decreases when the water potential drops below -1 to -3 bars (Busby & Whitfield 1978), drought-tolerant mosses can resume normal photosynthesis after a drop in water potential to about -1000 bars, a condition found during the dry, hot days of summer in the open (Dilks & Proctor 1979). Even in the shaded forest, the water potential of a moss can drop to -200 to -400 bars. While flowering plants and ferns may have negative photosynthesis at water potentials of -12 to -15 bars, mosses such as the woodland to semi-shaded species ***Hylocomium splendens*** (Figure 61-Figure 62), ***Pleurozium schreberi*** (Figure 64), and ***Tomenthypnum nitens*** (Figure 65) can continue net photosynthesis until the water potential falls below -55 to -100 bars (Busby & Whitfield 1978), and ***Camptothecium lutescens*** (Figure 66) from the United Kingdom can maintain a net positive photosynthesis down to -150 bars (Dilks & Proctor 1979). The drought-intolerant moss ***Hookeria lucens*** (Figure 67), on the other hand, must maintain 100% humidity and cannot maintain positive photosynthetic gain when the water potential drops below 80 bars (Dilks & Proctor 1979). Yet this highly drought-intolerant moss, relatively speaking, has primary cell walls with **pit fields** in its stem parenchyma, structures common to tracheids and vessels and permitting lateral transport, suggesting that ***Hookeria lucens*** may use these cells in internal conduction (Cortella *et al*. 1994).

Figure 64. ***Pleurozium schreberi***, an ectohydric moss with leaves completely covering the stem. Photo by Janice Glime.

Figure 65. ***Tomentypnum nitens***, an ectohydric moss. Note dense tomentum covering stems. Photo by Michael Lüth, with permission.

One adaptation to maintaining water is to increase the osmotic value of the cells. Ochi (1952) compared a number mosses and showed that the highest osmotic values were generally in mosses adapted to xeric conditions. He obtained high values (0.90-0.62) in such tree-trunk and sunny rock dwellers as ***Hedwigia ciliata*** (Figure 82), ***Thamnobryum subseriatum*** (=*Thamnobryum sandei* var. *cymbifolium*?) (Figure 68), ***Myuroclada maximowiczii*** (Figure 69), ***Thuidium cymbifolium*** (Figure 70), ***Neckera yezoana***, and ***Anomodon giraldii*** (Figure 71). Intermediate values characterized those on soil (0.70-0.30), including ***Dicranum japonicum*** (Figure 37), ***Pogonatum inflexum*** (Figure 72), ***Plagiomnium maximoviczii*** (Figure 73), and ***Plagiomnium cuspidatum*** var. ***trichomanes*** (Figure 74). In shady, wet, forested areas, Ochi obtained the lowest value (0.26), exemplified by ***Plagiomnium vesicatum*** (Figure 75) and ***Hookeria acutifolia*** (Figure 76). Surprisingly, values were highest in older plants and mature portions, not the vital young buds.

Figure 66. ***Camptothecium lutescens***, a moss that can maintain photosynthesis at very low water potential. Photo by Michael Lüth, with permission.

Figure 67. ***Hookeria lucens***, showing thin leaves that are very drought-intolerant. Photo by Michael Lüth, with permission.

Figure 68. ***Thamnobryum subseriatum***, a moss from emergent rocks of streams. Photo by Michael Lüth, with permission.

Figure 69. ***Myuroclada maximoviczii***, a rock dweller with high osmotic values. Photo by Janice Glime.

Figure 70. ***Thuidium cymbifolium***, a sunny rock dweller with high osmotic values, with capsules. Photo by Li Zhang, with permission.

Figure 71. ***Anomodon giraldii***, a xerophyte. Photo by Misha Ignatov, with permission.

Figure 72. ***Pogonatum inflexum***, an endohydric soil moss. Photo from Digital Museum, Hiroshima University, with permission.

Figure 73. ***Plagiomnium maximoviczii***, an endohydric species. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Figure 74. ***Plagiomnium cuspidatum***, a soil moss with endohydric water transport. Photo by Hermann Schachner, through Creative Commons.

Figure 75. ***Plagiomnium vesicatum***, an endohydric moist forest soil moss. Note the wide spacing of the leaves – a morphology that is unsuitable for good ectohydric transport. Photo from Digital Museum, Hiroshima University, with permission.

Figure 76. ***Hookeria acutifolia***, a moist forest species with poor desiccation tolerance. Photo by Steve Joya, permission pending.

Proctor (1999) likewise examined a number of bryophytes to determine their osmotic potential. He found that the leafy ones (mosses and leafy liverworts) have a full turgor osmotic potential of -1.0 to -1.5 MPa, whereas the multistratose thallose liverworts have -0.5 to -1.0 MPa.

The full turgor content of water varies with season, ranging 100-300% in bryophytes from well-drained habitats. But Proctor found that the highest turgor occurs in the new growth. The cell walls are highly extensible in most of the thallose liverworts and such drought-tolerant mosses as ***Syntrichia ruralis*** var. ***arenicola*** (Figure 77) and ***Racomitrium lanuginosum*** (Figure 78), but it is quite low in certain leafy liverworts with very rigid cell walls. Unlike Ochi (1952), Proctor found that variations in water relation parameters seem to bear little relationship to habitat for most bryophytes. He attributed this lack of relationship to the consideration that they are usually only metabolically active when they are fully hydrated.

Some bryophytes can tolerate turgor up to 1400% of their dry mass [***Dumortiera hirsuta*** (Figure 79) & ***Conocephalum conicum*** (Figure 80)] (Proctor *et al*. 1998). On the other hand, xerophytic mosses such as ***Syntrichia ruralis*** (Figure 77) and ***Andreaea alpina*** (Figure 81) reach full turgor at only 110%.

Figure 77. ***Syntrichia ruralis*** var. ***arenicola***, a drought-resistant moss with very extensible cell walls. Photo by Michael Lüth, with permission.

Figure 78. ***Racomitrium lanuginosum***, a drought-resistant moss with very extensible cell walls. Photo by Janice Glime.

Water Content

Given sufficient water, water content is related to the cell's osmotic potential. Low water content seems to be related to a xeric habitat (Hernández-Garcia *et al*. 1999), suggesting tolerance rather than the avoidance that might be obtained by maintaining high osmotic potential. In the xeric and mesic pine forests of Tenerife, water content of all mosses tested was <140% of dry mass. ***Hedwigia ciliata*** (Figure 82), ***Grimmia laevigata*** (Figure 83), ***G. trichophylla*** (Figure 84), and ***Pterogonium gracile*** (Figure 85), the rock dwellers, have the lowest field water content and fastest absorption and water loss rates among the species. ***Polytrichum juniperinum*** (Figure 86), ***Bartramia stricta*** (Figure 87), and ***Anacolia webbii*** (Figure 88) have the highest field water content and slowest water absorption and loss rates. The highest drought tolerance occurs in ***H. ciliata***, ***B. stricta***, ***G. laevigata***, and ***G. trichophylla***.

Figure 79. ***Dumortiera hirsuta*** showing hairs on edges of thalli and a turgid condition. Photo by Li Zhang, with permission.

Figure 80. ***Conocephalum conicum***, a liverwort that can tolerate turgor up to 1400% of its dry mass. Photo by Dick Haaksma, with permission.

Figure 81. ***Andreaea alpina***, a xerophytic moss that can only tolerate turgor up to 110% of dry weight. Photo by Andrew Hodgson, with permission.

Figure 82. ***Hedwigia ciliata***, a very drought-tolerant species. Photo by Michael Lüth, with permission.

Figure 83. ***Grimmia laevigata***, a rock-dweller with low water content and rapid water uptake. Photo by Jonathan Sleath, with permission.

Figure 84. ***Grimmia trichophylla***, a rock-dweller with low water content and rapid water uptake. Photo by Michael Lüth, with permission.

Figure 85. ***Pterogonium gracile***, a rock-dweller with low water content and rapid water uptake. Photo by David Holyoak, with permission.

Figure 86. ***Polytrichum juniperinum***, an endohydric moss with high water content and slow water absorption. Photo by Keith Bowman, with permission.

Figure 87. ***Bartramia stricta***, a moss with high water content and slow water absorption. Photo by Michael Lüth, with permission.

Figure 88. ***Anacolia webbii***, a rock-dweller with low water content and rapid water uptake. Photo by Jan-Peter Frahm, with permission.

Nevertheless, most bryophytes apparently do not exhibit the low **water capacity** (50-250%) that permits some seed plants and lichens to survive areas with very low rainfall (During 1992). Known **water capacities** (percent of wet mass relative to dry mass) in bryophytes mostly fall into the high water capacity range of 650-1700% (During 1992), except for endohydric taxa, ranging 190-577% (Coufalová 1951). For example, the damp forest leafy liverwort ***Bazzania trilobata*** (Figure 89) at saturation had a moisture content of 1300% of its dry mass (Sollows *et al*. 2001).

Figure 89. ***Bazzania trilobata***, a damp forest species with a saturation moisture content of ~1300% dry weight. Photo by Jan-Peter Frahm, with permission.

Nichols (1918) reported that ***Sphagnum*** (Figure 63) pads, used for bandages in World War I, could absorb up to 22 times their mass (water capacity = 2200%), making them 5-6 times as absorptive as cotton pads. Other bryophytes, as in some South African montane areas, survive on the water they collect from early morning mist in low-lying clouds (Russell 1982), suggesting that these bryophytes may indeed have low water capacities. Furthermore, many bryophyte taxa are tolerant of very low water contents (5-10% of dry mass), resuming photosynthesis upon remoistening (Proctor 1990).

It appears that at least for some bryophytes, it is best to be wet or be very dry. Water pressure in the range of –100 to –200 MPa is best for survival in a dry state (Proctor 2001). Akande (1984, 1985) has examined the effects of the degree of dehydration on Nigerian bryophytes and found that those maintained at 0% humidity for one week and for one month both resumed respiration more quickly than those maintained for the same time period at 32% and 54% (Akande 1984). He found that the leafy liverwort ***Mastigolejeunea florea*** is less desiccation-tolerant than the two mosses studied, but all three taxa did have individuals that survived at 0%, 32%, and 54% relative humidity at ambient temperature (Akande 1985).

Water-logging

Despite their needs for high water content, bryophytes cannot afford to be too wet or they are unable to carry out photosynthesis. Acquiring CO_2 must occur through the leaf surface, and a continuous layer of water interferes with that transfer. Silvola (1991) found that in all the boreal forest mosses he tested except ***Polytrichum commune*** (Figure 54-Figure 55), photosynthesis decreased when the water content exceeded a certain optimal level (see also Williams & Flanagan 1991). It is likely that the leaf lamellae provided air spaces for CO_2 transfer in ***P. commune***. Many ***Sphagnum*** species suffer similarly from water-logging.

Inducible vs Constitutive Desiccation Tolerance

As recently as 2011, Green *et al*. reviewed the literature and reported that bryophytes appear to all be constitutive. To support this they cite that no protein synthesis is required upon rehydration before metabolism can commence. Bryophytes furthermore appear to always be protected from desiccation mortality. Further support is the constant presence of high sucrose levels. And the cellular structure is usually maintained during desiccation.

Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] **desiccation tolerance** exist among bryophytes (Stark *et al*. 2013). Those with **constitutive desiccation tolerance** (**CDT**) are not dependent on the rate of drying to determine their recovery, whereas those that depend on **inducible desiccation tolerance** (**IDT**) are. Reduced or no desiccation tolerance following rapid drying is generally an indicator that the plants are IDT plants. Tracheophytes, with the exception of some ferns (Watkins *et al*. 2007), are IDT plants (Oliver *et al*. 1998, 2000), whereas bryophytes are mostly CDT plants (Toldi *et al*. 2009), hence their high ability to survive drying.

Those bryophytes with **constitutive desiccation tolerance** (**CDT**) are not dependent on the rate of drying, whereas those with only **inducible desiccation tolerance** (**IDT**) are. Therefore, the IDT plants, including IDT bryophytes, are likely to die when exposed to rapid drying.

But bryophytes can use both strategies. Stark and coworkers have investigated the inducible protections that permit bryophytes to survive desiccation. Those bryophytes that survive slow drying but not rapid drying provide us with evidence that something happens during that slow drying process, and that happening provides the inducible desiccation tolerance (Stark *et al*. 2013). Bryophytes also possess constitutive desiccation tolerance, a tolerance that is common among terrestrial bryophytes. For example, the desert moss ***Pterygoneurum lamellatum*** (**Pottiaceae;** Figure 7) exhibits both a constitutive and an inducible response. The bryophyte tolerance strategy couples **constitutive** cellular protection during dehydration with the **induction** of a recovery/repair mechanism upon rewetting (Oliver *et al*. 2005; Toldi *et al*. 2009; Stark & Brinda 2015).

More recently, Stark and Brinda (2015) have found that not only can a desert moss have both inducible and constitutive desiccation tolerance, but it can have each in different parts of the same shoot at the same time or in different stages in the life cycle. Stark and Brinda propose that as the sporophyte grows older, the presence of sugars in the sporophyte facilitates desiccation tolerance. This would help to explain the greater danger of death by desiccation in the early embryonic stage before significant sugar accumulation occurs. At the same time, the early embryo exhibits inducible desiccation tolerance (IDT) and requires slow desiccation, usually not a problem within the protection of the apical gametophyte leaves. As the embryo develops and the seta emerges from these protective leaves, the sporophyte changes from IDT to partially CDT. Stark and Brinda suggest that this evolutionary change resulted from selection pressures of intermittent drying in this exposed sporophyte. This exposed sporophyte tissue is most likely subject to faster rates of desiccation, making an inducible system inadequate to meet the time demands and selecting for the constitutive desiccation tolerance. The presence of a waxy cuticle in the capsules of ***Funaria hygrometrica*** (Figure 26) provide an example of this CDT (Budke *et al*. 2011, 2012, 2013).

Stark and Brinda (2015) concluded that once the seta elongation phase reaches the stage of capsule expansion, sucrose imported from the gametophyte (Renault *et al.* 1992) should be present in the sporophyte, endowing the sporophyte with the raw materials needed to tolerate rapid drying (Stark & Brinda 2015). In ***Acaulon muticum*** (Figure 92), small vacuoles are present in the placental region of the sporophyte-gametophyte junction (Rushing & Anderson 1996). These abundant vacuoles may be present in the embryonic sporophyte as well, where they could provide protection from water stress in the rapidly growing sporophyte.

Wolkers *et al*. (2001) had already suggested that a slower rate of drying may permit the proteins and sucrose to interact in a more protective manner. For example, in ***Physcomitrella patens*** (Figure 21, Figure 90) and ***Syntrichia ruralis*** (Figure 93), a slow drying treatment induces the production of either ABA (see below) or dehydrin, or both (Werner *et al.* 1991; Hellwege *et al.* 1994; Cuming *et al*. 2007). When ABA is applied to the outside of ***Exormotheca holstii*** (Hellwege *et al.* 1994), it elevates sucrose levels and increases protection against rapid drying (see also Pence 1998; Oldenhof *et al.* 2006). Koster *et al*. (2010) demonstrated the genetic connection between ABA and the expression of several homologs to stress proteins, including two dehydrin-like proteins. The only problem with this logic is that the natural presence of ABA is still unknown in ***Physcomitrella patens*** and ***Syntrichia ruralis*** (Stark & Brinda 2015).

Figure 90. ***Physcomitrella patens*** sporophyte, a species in which a slow drying treatment induces the production of either ABA or dehydrin. Photo from Ralf Reski Lab, through Wikipedia Commons.

In ***Aloina ambigua*** (Figure 91), Stark and Brinda (2015) considered that the seta may elongate too fast for the inducible desiccation tolerance system to respond. This exposed tissue may therefore rely on the constitutive system to provide desiccation tolerance for the developing capsules.

Figure 91. ***Aloina ambigua*** with capsules. The seta may grow too rapidly in this species for inducible desiccation tolerance to protect it. Photo by Michael Lüth, with permission.

Hardening

Hardening is a phenomenon known for flowering plants, but the concept is usually associated with preparation for winter. Beckett *et al*. (2005) induced desiccation hardening in the moss ***Atrichum androgynum*** (Figure 11) by reducing the relative water content of apical portions for 1/2 to 3 days, followed by storage fully hydrated for another day. Plants were then desiccated for 16 hours over silica gel, and the recovery of PSII during rehydration was monitored. Hardening affected photosystem II (PSII) before desiccation, decreasing its efficiency, especially at saturating light intensities. Upon rehydration, however, hardened plants recovered their PSII activity more quickly and greatly increased the non-photochemical quenching in the first few hours compared to those plants not subjected to hardening. Beckett *et al*. concluded that hardening shifts the photosynthetic apparatus from a state of high efficiency to one of less efficiency but having a photoprotected state.

Hardening can confound physiological experiments when comparing desiccation tolerance. Once hardened, the plant is likely to receive the benefits in desiccation resistance for a prolonged period of time, such that a rehydration period of 24-72 hours may not remove that benefit (Bopp & Werner 1993; Stark *et al*. 2014). Instead, regenerates from fragments (regenerated more than once to eliminate prior hardening) or plants grown from spores may be necessary to create plants that have no prior desiccation experience, hence no hardening (Stark & Brinda 2015).

Figure 92. ***Acaulon muticum***, a species with small vacuoles in the placental region that may protect the sporophyte from water stress. Photo by Michael Lüth, with permission.

Desiccation-induced Changes

Iljin (1953, 1957) considered that mechanical injury to the protoplast membranes during the drying and rewetting processes is the primary cause of desiccation sensitivity. He considered the tensions that develop in cells during dehydration, pulling protoplasm inward as the vacuoles shrink and cell walls pulling membranes outward, are the primary causes of lethal injuries in drought-sensitive species. Drought-tolerant plants mitigate these tensions by such cellular aspects as reduced cell size, small or absent vacuoles, lack of plasmodesmata, easily deformed cell walls, and reduced osmotic pressure. For example, small cytoplasmic vesicles (vacuoles) are present in such desiccation-tolerant species as ***Syntrichia ruralis*** (Figure 93), ***Neckera crispa*** (Figure 94), ***Pleurozium schreberi*** (Figure 64), and ***Triquetrella papillata*** (Figure 95) (Oliver & Bewley 1984). But this does not hold true for all species – in the desiccation-tolerant ***Ceratodon purpureus*** (Figure 96-Figure 98) and ***Didymodon vinealis*** (Figure 99), the vacuoles are quite large. And the desiccation-intolerant ***Cratoneuron filicinum*** (Figure 40) does not have large vacuoles. **Plasmodesmata** (microscopic channels that traverse cell walls of plant and some algal cells, enabling transport and communication between them) likewise do not seem to be related to desiccation-tolerance, but these are difficult to see and often require electron microscopy for viewing.

Figure 93. ***Syntrichia ruralis***, a species in which slow drying induces the production of ABA. Photo by John Game, with permission.

Figure 94. ***Neckera crispa***, a species with small cytoplasmic vesicles (vacuoles). Photo by David Holyoak, with permission.

Figure 95. ***Triquetrella papillata*** from New Zealand, a species with small cytoplasmic vesicles (vacuoles). Photo by Jan-Peter Frahm, with permission.

Figure 96. ***Ceratodon purpureus***, a desiccation-tolerant species dry on a rock. Photo by Michael Lüth, with permission.

Figure 97. ***Ceratodon purpureus*** hydrated on a rock. Photo by Michael Lüth, with permission.

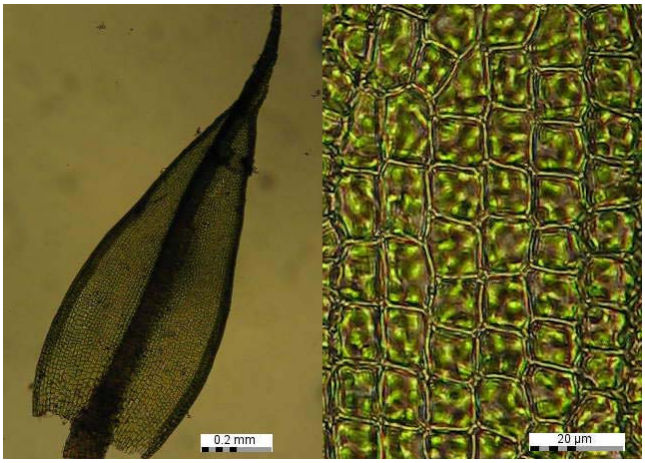

Figure 98. ***Ceratodon purpureus*** leaf and leaf cells, a desiccation-tolerant species with large vacuoles. Photo by Tom Thekathyil, with permission.

Figure 99. ***Didymodon vinealis***, a desiccation-tolerant species with large vacuoles. Photo by Michael Lüth, with permission.

Henckel and Pronina (1968, 1969, 1973) suggest that those plants that are drought-tolerant are continuously prepared for desiccation, *i.e.*, have constitutive desiccation tolerance. However, this theory likewise did not fit the evidence presented by slow vs rapid drying in bryophytes. Bewley (1979) suggested that instead, three factors are critical to desiccation tolerance:

1. limiting damage during desiccation to a reparable level
2. maintaining physiological integrity in the dry state so that metabolism can be reactivated quickly upon rehydration
3. putting repair mechanisms into effect upon rehydration, in particular to retain or regain integrity of membrane and membrane-bound organelles.

As bryophytes desiccate, a series of changes occurs. In ***Physcomitrella patens*** (Figure 21, Figure 90), these changes include plasmolysis, chloroplast remodelling, and microtubule depolymerization, as demonstrated by desiccation for more than one month to 10% of fresh weight (Wang *et al*. 2009). Nevertheless, Wang and coworkers found that the membranes retain their integrity. These changes involved 71 responsive proteins. Most of these were involved in metabolism, cytoskeleton, defense, and signaling. But not all changes seem to be that of repair

or stability. Cytoskeletal protein degradation might cause cytoskeletal disassembly and resulting changes in cell structure. **Late embryogenesis abundant proteins (LEA proteins)** and reactive oxygen species-scavenging enzymes are among those prominently induced, possibly helping to reduce the damage caused by desiccation. Oliver *et al*. (2004) likewise found that the LEA proteins were the most abundant transcripts associated with drying tissues. They suggest that the LEA proteins might play a role in recovery from desiccation.

Oliver *et al*. (2004) took a genetic approach to understanding desiccation tolerance, using the desiccation-tolerant ***Syntrichia ruralis*** (Figure 93). They found that the **transcriptome** (set of all RNA molecules, including mRNA, rRNA, tRNA, and other non-coding RNA transcribed in a cell) has a diverse population of transcripts that reflects a period of metabolic upheaval in the gametophyte cells. Much of the emphasis in this transcriptome is on the protein synthesis machinery, ion and metabolite transport, and the biosynthesis and repair of membranes. When gametophytes are rehydrated, there is a large number of transcripts that code for enzymes involved in oxidative stress metabolism and phosphorylating activities.

When ***Pterygoneurum lamellatum*** (Figure 7) is subjected to very rapid drying, it is severely damaged throughout the entire shoot except the shoot apex (Stark *et al*. 2013). This damage results in slower growth rates, fewer regenerative shoots, and a damaged photosynthetic system as demonstrated by alterations in fluorescence.

Cell Contents

As one might expect, cell contents respond to desiccation stress. In the mosses ***Bryum argenteum*** (Figure 100) and ***Didymodon vinealis*** (Figure 101) from cryptogamic crusts, the free proline content was significantly greater than in those from a typical (wetter) grassland (Xu *et al*. 2005).

Figure 100. ***Bryum argenteum*** in crack in parking lot, a species that manufactures proline in dry habitats. Photo by Paul Davison, with permission.

In the moss ***Plagiomnium acutum*** (Figure 103), concentrations of proline, soluble sugar, and reducing sugar all increase noticeably during dehydration, reaching maximum concentration after 12 hours (Li *et al*. 2009). As the membrane permeability increases, activities of protective enzymes likewise increase, including SOD, CAT, and POD. DNA degrades gradually, with only some of the low molecular weight fragments remaining. Upon rehydration, all of these changes reverse. ***Physcomitrella patens***, like ***Plagiomnium acutum***, accumulates the osmoprotectants altrose, malitol, ascorbic acid, and proline when subjected to drought stress (Erxleben *et al*. 2012).

Figure 101. ***Didymodon vinealis***, a cryptogamic crust species that maintains high concentrations of proline in dry conditions. Photo by Michael Lüth, with permission.

Figure 102. ***Physcomitrella patens***, a species that accumulates altrose, malitol, ascorbic acid, and proline in response to drought stress. Photo by Michael Lüth, with permission.

Figure 103. ***Plagiomnium acutum***, a moss that demonstrates increases in proline, soluble sugar, and reducing sugar during desiccation. Photo by Liu; permission pending.

Cruz de Carvalho *et al*. (2015) found that the low water potentials in dehydrating cells of the aquatic moss ***Fontinalis antipyretica*** (Figure 104) is coupled with osmoregulation due to increase of such soluble materials a soluble sugars and compatible inorganic ions. These increase turgor pressure. In addition to its role as an osmolyte, sucrose stabilizes membranes and proteins through **vitrification**, *i.e.*, by creating glasslike substances. When the moss was dehydrated slowly, the cell walls became more elastic, permitting cell shrinkage that maintained turgor and helped to preserve metabolic functions. However, in rapid drying, there was a loss of turgor and osmotic potential. Although the sucrose content increased, rehydration of the fast-dried samples resulted in 50% loss of sucrose through cell leakage as a result of cell membrane rupture. Slowly dehydrated leaves, on the other hand maintained their sucrose content upon rehydration. The thick mats of long dangling ***Fontinalis antipyretica*** facilitates slow drying of this species in nature.

Sucrose acts as an osmotic "spacer" in membranes (Werner *et al*. 1991; Oldenhof *et al*. 2006; Cruz de Carbalho *et al*. 2014). This is accompanied by ABA mediation of protein synthesis, strengthening the cellular glasses typical of inducible desiccation tolerance in mosses, as shown in ***Physcomitrella patens*** (Oldenhof *et al*. 2006).

Chloroplast Responses

Bryophyte chloroplasts undergo ultrastructural changes when undergoing desiccation. Chloroplasts become smaller and more spherical with a less-well defined internal structure (Noailles 1978). The general lamellar structure collapses, with the **thylakoids** (chlorophyll vesicles) becoming dispersed; starch granules are lost. This response is similar to that induced by ABA in experiments related to freezing tolerance (Nagao *et al*. 2005).

Bryophyte chloroplasts contain **plastoglobuli** (Tucker *et al*. 1975; Oliver & Bewley 1984) in groups within the stroma. These increase in size and number during dehydration in ***Syntrichia ruralis*** (Figure 93) (Tucker *et al*. 1975).

It appears that the chloroplasts may be altered by desiccation in other ways we do not fully understand. I found that I could not extract chlorophyll effectively from dry ***Fontinalis*** spp. (Figure 104) using acetone unless I rewet them for about 15 seconds first. Tuba (1984) reported a possible decoupling of the chlorophyll from its protein, but later (Tuba 1985) attributed that apparent phenomenon to the separation of upper and lower shoots and the extraction process. In fact, he stated that the chlorophyll *a* and *b* remained unchanged during daily desiccation and early rehydration of ***Syntrichia ruralis*** (Figure 93). He concluded that the **neoxanthin** (a carotenoid pigment), due to its hydrophilous nature, may be adaptive in binding the **LHCP** (light-harvesting chlorophyll protein) to the **PS II** chlorophyll core, thus stabilizing the LHCP.

One factor in the protection of chlorophyll against light damage during desiccation is that the pigment **zeaxanthin** can bind to the chlorophyll-containing thylakoid protein (Deltoro *et al.* 1998; Heber *et al*. 2001). On the other hand, loss of chlorophyll fluorescence during drying of pre-darkened mosses suggests that energy dissipation in the desiccated mosses is unrelated to zeaxanthin availability.

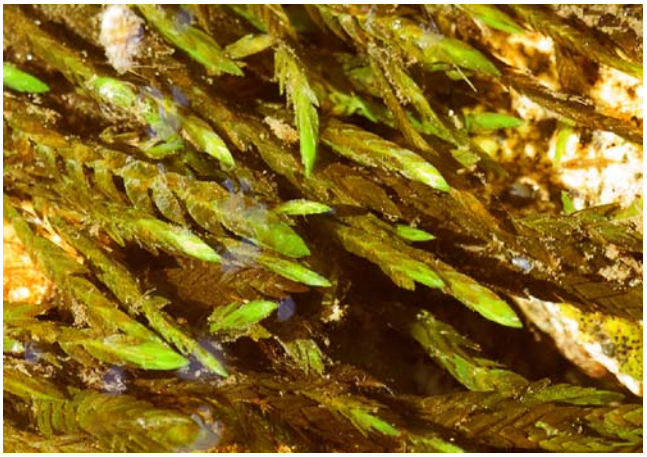

Figure 104. ***Fontinalis antipyretica***, a moss that, when dry, has a delay before its chlorophyll dissolves in alcohol, suggesting that the chlorophyll may be complexed during dehydration. Projecto Musgo, through Creative Commons.

Even among the desiccation-tolerant bryophytes, the rate of recovery of chlorophyll fluorescence varies widely upon rehydration (Proctor 2010). For example, some species have high values of F_v/F_m in the early minutes of recovery, accompanied by low absolute values of F_m. But most recovery curves are logistic (S-shaped curve that starts slow, goes up exponentially, than approaches horizontal) for photosynthetic CO_2 fixation in the light.

Photosynthesis

Lee and Stewart (1971), using ***Calliergonella cuspidata*** (Figure 58), ***Climacium dendroides*** (Figure 105), and ***Hypnum cupressiforme*** (Figure 46-Figure 47), found that the degree of desiccation tolerance correlates with the degree of moisture stress experienced in the habitat. This tolerance is expressed as a rapid recovery of photosynthetic rate in taxa from habitats with severe moisture deficits, whereas those from habitats with no appreciable moisture deficits lose photosynthetic capability more quickly and are slower to recover.

Seel *et al*. (1992) made similar comparisons using ***Syntrichia ruralis*** (Figure 93), ***Bryum pseudotriquetrum*** (Figure 106), and ***Dicranella palustris*** (Figure 107) from a range of habitats with different water availabilities. All three species become photosynthetically inactive when dried to a water content of 100-200%. But recovery differs. The xeric ***Syntrichia ruralis*** from sand dunes recovers to its pre-desiccation photosynthetic rates, but its rate of recovery is affected by irradiance during its desiccation. Those mosses from hydric habitats, when rehydrated, have partial resumption of their photosynthetic electron transport if they are dried in the dark, but if they are dried in even low light they did not resume their photosynthetic activity. Their symptoms indicate a lasting photoinhibition of photosynthesis following rehydration. On the other hand, the desiccation-tolerant ***Syntrichia ruralis*** (Figure 93) experiences significant photoinhibition only when receiving continuous high irradiance (1200 $\mu mol\ m^{-2}\ s^{-1}$) while hydrated. But if it is dehydrated while receiving high irradiance it shows less evidence of photoinhibition after rehydrations. Desiccation at low irradiance has no effect following rehydration. Leaf curling reduces photon flux absorption by 50-60% in dry mosses compared to hydrated mosses, although it is

possible that changes in optical properties of papillae may contribute to that reduction.

Figure 105. ***Climacium dendroides***, a species that shows acclimation to its habitat adjusting its tolerance to the moisture stress experienced in the habitat. Photo by Michael Lüth, with permission.

Figure 106. ***Bryum pseudotriquetrum***, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.

Figure 107. ***Dicranella palustris***, a species that becomes photosynthetically inactive when its water content is decreased to 100-200%. Photo by Michael Lüth, with permission.

Both thylakoid lipids and chlorophyll reduction coincide with the loss of photosynthesis in dehydrating ***Atrichum androgynum*** (Figure 11) (Guschina *et al*. 2002).

The desert moss ***Syntrichia caninervis*** (Figure 12) recovers quickly when shoots are remoistened in the dark (Zhang *et al*. 2011). This is an advantage for this moss that receives much of its moisture from dew, a night-time phenomenon. Its leaf hairs are able to trap the dew (and also fog and raindrops) and direct them to the base of the leaf where it rapidly is absorbed. The chlorophyll fluorescence has a narrow optimum range. The moss seems to experience no damage to its membranes or organelles and reaches 90% of its 30-minute photosynthetic yield within the first minute of rehydration. This permits it to take rapid advantage of small amounts of moisture from fog, dew, snow, and short rainfall events.

Mitochondria

The mitochondria [cell organelle that generates most of the cell's supply of **ATP** (adenosine triphosphate), used as a source of chemical energy] become deformed as they dehydrate, becoming small and rounded (Noailles 1978). Internal cristae may be greatly reduced in size or lost completely.

Nuclei

The nuclei seem to suffer little from the effects of desiccation, retaining their normal size (Noailles 1978).

Vacuoles and Vesicles

Normal bryophyte cells have one to several large vacuoles (Noailles 1978). During dehydration, these break down to form numerous small vesicles (Oliver & Bewley 1984). It appears that ABA may be involved in this transformation, since the response is similar to that induced by ABA during freezing (Nagao *et al*. 2005). ABA-treated cells have slender chloroplasts, and the quantity of starch grains is reduced in comparison with those of non-treated cells.

Membranes

Membranes in general suffer from dehydration, including thylakoids, cristae, and cytoplasmic membranes like endoplasmic reticulum and dictyosomes, resulting in the shrinkage of organelles (Noailles 1978). The chloroplast membrane itself may exhibit clefts (Tucker *et al*. 1975). It is the ability to repair this damage that makes many bryophytes desiccation tolerant (Li *et al*. 2009).

Both desiccation-tolerant and intolerant bryophytes leak electrolytes when rehydrated (Gupta 1976, 1977, 1979), as do dry viable seeds, lichens, pollen grains, fungi, and their spores (Simon 1974, 1978). This leakage lasts only a few minutes except in cases of permanent damage (Oliver & Bewley 1984). Oliver and Bewley (1984) listed amino acids, mono-, di-, and tri-saccharides, sugar alcohols, organic acids, hormones, phenolics, phosphates, and various electrolytes as leaked substances during rehydration, although the leakage often lasts only minutes.

The desert moss ***Syntrichia caninervis*** (Figure 12) is the dominant species in the Gurbantunggut Desert, a cold desert in Central Asia. Wu *et al*. (2012) investigated the

membrane changes during desiccation of this species. There are no significant changes in electrical conductivity of the rehydration water during dehydration or rehydration. There also appears to be no ultrastructural damage to the membrane during dehydration or rehydration, but there are major changes in cellular ultrastructure. Wu and coworkers suggest three possible explanations for the apparent disruption of the membranes in desiccated state:

1. Adaptive morphological features of the leaf that remain intact permit the leaves to regain membrane integrity rapidly upon rehydration.
2. The moss becomes dormant rapidly, maintaining some level of membrane integrity.
3. Soluble sugars and free **proline** (constitutive substances) increase rapidly during desiccation, contributing to membrane stabilization.

Plasmolysis

One of the consequences of desiccation can be **plasmolysis** of the cells (shrinkage of protoplast away from cell wall) (Oliver & Bewley 1984). In some cases, very narrow elongate cells seem to resist plasmolysis, perhaps due to the small cell volume and strong adhesion to the cell walls. But plasmolysis can occur in bryophytes and can result in cell damage to both the plasma membrane and the cell wall.

In ***Didymodon vinealis*** (Figure 99) and ***Triquetrella papillata*** (Figure 95), the dehydrated cells contract to 50-70% of the original volume (Moore *et al*. 1982). The cell walls contract, permitting the protoplasm to fill the cell and preventing entry of air into the drying cells.

It appears that at least the liverwort ***Sphaerocarpos donnellii*** (Figure 108) is able to partially compensate for this plasmolysis damage (Grusak *et al*. 1980), where both normal and plasmolyzed tissues are composed primarily of hemicellulose and cellulose. But in plasmolyzed cells, labelled C^{14} is considerably lower than in normal cells. Rather, these cells have higher radioactivity in pectin and hemicellulose and less in cellulose, suggesting a possible mechanism for enhancing wall stability. This transformation would provide numerous sites for cross-linkage between the cellulose microfibrils as walls regenerate.

Figure 108. ***Sphaerocarpos donnellii***, a species that has the ability to partially compensate for plasmolyzed cells. Photo by Belinda Lo, through Creative Commons.

Liverworts

Liverworts have received surprisingly little attention relative to their drought tolerance strategies. Granted, these plants seem to require higher moisture conditions in general, but their presence as epiphytes in many areas attests to the ability of at least some liverworts to survive long periods of drought, and certainly the thallose liverworts of flood plains and other seasonal habitats provide another set of highly desiccation tolerant or desiccation avoider species.

Pressel *et al*. (2009) found that liverworts undergo "profound" cytological changes during dehydration. As in tracheophytes and mosses, these include fragmentation of the vacuole, rounding of chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged. Furthermore, chlorophyll fluorescence returns to normal within 24-48 hours during rehydration. And like the mosses, their dehydration and rehydration are associated with the depolymerization and repolymerization of the cortical microtubule cytoskeleton. But unique among the bryophytes is the presence of **oil bodies** in liverworts, membrane-bound organelles that take on many shapes among the species (Kozlowski 1921; Kis & Pócs 1997). And these cellular inclusions, long considered only for their taxonomic value, seem to have an important role in liverwort recovery from dehydration (Pressel *et al*. 2009).

Taxonomists have been aware that these oil bodies usually disappear in herbarium specimens, and that they do not reappear upon re-wetting and microscopic observation. But it appears that to see these in herbarium specimens, one must treat the liverworts as nature does – dry them slowly and give them time to recover upon rehydration. It turns out that they remain largely unchanged while they are dry (Pressel *et al.* 2009), but who observes dry specimens under the microscope? Rather, they become flattened when rehydrated and in the six liverworts tested, they require 48 hours to regain their normal shapes, long after the taxonomist has cleaned the microscope slide. Fast drying causes them to disintegrate upon redrying, along with other liverwort organelles. Pressel *et al.* interpreted this initial loss of shape upon rewetting to indicate a shift in soluble carbohydrates or other components into the cytosol, suggesting that these may be crucial energy reserves needed for recovery and desiccation tolerance.

Kronestedt (1983) found that there was seasonal variability in the oil bodies of the floating liverwort ***Ricciocarpos natans*** (Figure 109). But as He *et al*. (2013) made clear, the function of oil bodies in most liverworts still remains unclear.

Figure 109. ***Ricciocarpos natans***, a species with seasonal variability of oil bodies. Photo by Norbert Stapper, with permission.

Habitat Relations

In their review of lichen and bryophyte desiccation and rehydration, Green *et al*. (2011) considered that the rate of recovery may relate to the length of the hydrated activity period. They reported that species that hydrate and then dry rapidly (*e.g*. rock surfaces) recover rapidly. By contrast, those species from habitats that remain wet for a long time recover from dryness more slowly when rehydrated.

Cruz de Carvalho *et al*. (2014) found that even the aquatic moss ***Fontinalis antipyretica*** (Figure 104) can survive slow dehydration, during which both dehydration and rehydration proteins are induced. These protein profiles are similar to those of the terrestrial moss ***Physcomitrella patens*** and ***Syntrichia ruralis***. The proteins associated with photosynthesis and the cytoskeleton were reduced during dehydration. In their place, the cells accumulated proteins involved in sugar metabolism and plant defenses. Upon rehydration the protein accumulation patterns for photosynthesis and the cytoskeleton return to normal levels. However those for sugar accumulation and defense remain high. During fast dehydration, on the other hand, this moss exhibited little change in proteins. Upon rehydration, proteins were leaked. The researchers suggested that bryophytes from contrasting habitats may share common desiccation tolerance mechanisms.

Summary

Bryophytes may be **desiccation tolerant**, surviving dry tissues and beginning photosynthesis upon rehydration, or they may be **drought avoiders**, using structural adaptations and life cycle stages to escape having a dry vegetative plant. The presence of a **central strand** does not seem to correlate with the degree of internal conduction, but habitat does.

Life cycles are a major protector against dry seasons, permitting bryophytes to survive as tubers, gemmae, spores, fragments, and buds. These stages are typically timed to coincide with drought seasons. They are likely to be combined with physiological changes, including dormancy, in the plants as they respond to changes in the environment.

Xeric bryophytes are more likely to have greater internal conduction and faster external conduction than mesic and hydric taxa. It is possible that the central strand may serve as a water reservoir in some taxa. Physiologically, some bryophytes can increase the osmotic value of the cells, and they typically have a high water capacity compared to drought-tolerant seed plants. Desiccation tolerance permits some bryophytes to remain dormant in a vegetative state for as many as 23 years.

During drying, chloroplasts undergo ultrastructural changes, **mitochondria** become **deformed**, and **vacuoles break down** to form smaller vesicles. Nuclei seem to remain intact. At least some taxa apparently protect their cell membranes from oxidative destruction. **ABA** seems to induce the production of H_2O_2 in light, reduce the loss of K^+, and may facilitate the reduction of oxygen release from photosystem II. Despite these adaptations, plasmolysis can occur and membranes can become damaged, requiring repair upon rehydration.

Liverworts may have one more trick in their cells – **oil bodies** that disappear rapidly upon rehydration, apparently converting oils into more usable forms of stored energy that could contribute to repair.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. I appreciate Lloyd Stark's generosity in sharing the information he found in reviewing papers and in summarizing the seeming conflicts in the literature regarding *Sphagnum*.

Literature Cited

Akande, A. O. 1984. Anhydrobiosis in corticolous bryophytes. Trop. Ecol. 25: 255-259.

Akande, A. O. 1985. Osmotic potential – A factor for resistance to water stress in some Nigerian species of corticolous bryophytes. Trop. Ecol. 26: 80-84.

Alpert, P. 1982. Poikilohydry and desiccation tolerance in some xerophytic mosses. Ph. D. Dissertation, Harvard University, Cambridge, pp. 19-31.

Alpert, P. 2000. The discovery, scope and puzzle of desiccation tolerance in plants. Plant Ecol. 151: 5-17.

Alpert, P. and Oechel, W. C. 1985. Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. Ecology 66: 660-669.

Anderson, L. E. and Bourdeau, P. F. 1955. Water relations in two species of terrestrial mosses. Ecology 36: 206-212.

Arts, T. 1986. Drought resistant rhizoidal tubers in *Fissidens cristatus* Wils. ex Mitt. Lindbergia 12: 119-120.

Arts, T. 1987. The occurrence of rhizoidal tubers in *Atrichum tenellum* (Roehl.) B. & S. and *A. crispum* (James) Sull. Lindbergia 13: 72-74.

Arts, T. 1988. The occurrence of drought-resistant rhizoidal tubers in *Haplodontium notarisii*. Lindbergia 14: 131-132.

Bates, J. W. 1997. Effects of intermittent desiccation on nutrient economy and growth of two ecologically contrasted mosses. Ann. Bot. 79: 299-309.

Beckett, R. P., Marschall, M., and Laufer, Z. 2005. Hardening enhances photoprotection in the moss *Atrichum androgynum* during rehydration by increasing fast- rather than slow-relaxing quenching. J. Bryol. 27: 7-12.

Becquerel, P. 1950a. La suspension de la vie au-dessous de 1/20ºK absolu par démagnétisation adiabatique de l'alun de fer dans le vide le plus élevé. Compte Rendu Hebd. Séances Acad. Sci. 231: 261-263.

Becquerel, P. 1950b. La vie latente des graines aux confins du zéro absolu. Compte Rendu Hebd. Séances Acad. Sci. 231: 1274-1277.

Becquerel, P. 1950c. La suspension de la vie des spores des Bactéries et des Moisissures desséchées dans le vide, vers le zéro absolu. Ses conséquences pour la dissémination et la conservation de la vide dans l'Univers. Compte Rendu Hebd. Séances Acad. Sci. 231: 1392-1394.

Becquerel, P. 1951. La suspension de la vie des Algues, Lichens, Mousses aux confins du zéor absolu et rôle de la synérèse réversible pour leur survie au dégel expliquant l'existence de la flore polaire et des hautes altitudes. Compte Rendu Hebd. Séances Acad. Sci. 232: 22-25.

Bewley, J. D. 1973. Desiccation and protein synthesis in the moss *Tortula ruralis*. Can. J. Bot. 51: 203-206.

Bewley, J. D. 1979. Physiological aspects of desiccation tolerance. Ann. Rev. Plant Physiol. 20: 195-238.

Bohnert, H. J. 2000. What makes desiccation tolerable? Genome Biol. 1: 1010.1-1010.4.

Bopp, M. and Werner, O. 1993. Abscisic acid and desiccation tolerance in mosses. Bot. Acta 106: 103-106.

Bowen, E. J. 1931. Water conduction in *Polytrichum commune*. Ann. Bot. 45: 175-200.

Bowen, E. J. 1933a. The mechanism of water conduction in the Musci considered in relation to habitat. I. Mosses growing in wet environments. Ann. Bot. 47: 401-423.

Bowen, E. J. 1933b. The mechanism of water conduction in the Musci considered in relation to habitat. II. Mosses growing in damp situations. Ann. Bot. 47: 635-661.

Bowen, E. J. 1933c. The mechanism of water conduction in the Musci considered in relation to habitat. III. Mosses growing in dry environments. Ann. Bot. 47: 889-912.

Breuil-Sée, A. 1993. Bryological notes – recorded desiccation-survival times in bryophytes. J. Bryol. 17: 679-684.

Bu, Z. J., X. X. Zheng, H. Rydin, T. Moore, and J. Z. Ma. 2013. Facilitation vs. competition: Does interspecific interaction affect drought responses in *Sphagnum*? Basic Appl. Ecol. 14: 574-584.

Budke, J. M., Goffinet, B., and Jones, C. S. 2011. A hundred-year-old question: Is the moss calyptra covered by a cuticle? A case study of *Funaria hygrometrica*. Ann. Bot. 107: 1279-1286.

Budke, J. M., Goffinet, B. and Jones, C. S. 2012. The cuticle on the gametophyte calyptra matures before the sporophyte cuticle in the moss *Funaria hygrometrica* (Funariaceae). Amer. J. Bot. 99: 14-22.

Budke, J. M., Goffinet, B., and Jones, C. S. 2013. Dehydration protection provided by a maternal cuticle improves offspring fitness in the moss *Funaria hygrometrica*. Ann. Bot. 111: 781-789.

Busby, J. R. and Whitfield, D. W. A. 1978. Water potential, water content, and net assimilation of some boreal forest mosses. Can. J. Bot 56: 1551-1558.

Charron, A. J. and Quatrano, R. S. 2009. Between a rock and a dry place: The water-stressed moss. Molec. Plant 2: 478-486.

Cortella, A., Ron, E., Estébanez, B., and Alfayate, C. 1994. On the occurrence of primary pit field cells in the caulidia of *Hookeria lucens* (Hedw.) Sm. (Bryopsida, Bryophyta). J. Hattori Bot. Lab. 77: 287-294.

Coufalová, E. 1951. Maximální vodní jímavost mechových polštářů a její hydrologický význam. Biologia (Bratislava) 12: 255-265.

Cruz de Carvalho, R., Bernades da Silva, A., Soares, R., Almeida, A. M., Coelho, A. V., Marques da Sliva, J., and Branquinho C. 2014. Differential proteomics of dehydration and rehydration in bryophytes: Evidence towards a common desiccation tolerance mechanism. Plant Cell Environ. 37: 1499-1515.

Cruz de Carvalho, R., Bernades da Silva, A., Branquinho, C., and Marques da Silva, J. 2015. Influence of dehydration rate on cell sucrose and water relations parameters in an inducible desiccation tolerant aquatic bryophyte. Environ. Exper. Bot. 120: 18-22.

Cuming, A. C., Cho, S. H., Kamisugi, Y., Graham, H., and Quatrano, R. S. 2007. Microarray analysis of transcriptional responses to abscisic acid and osmotic, salt, and drought stress in the moss, *Physcomitrella patens*. New Phytol. 176: 275-287.

Davey, M. C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25-31.

Deltoro, V. I., Calatayud, A., Gimeno, C., Abadia, A., and Barreno, E. 1998. Changes in chlorophyll *a* fluorescence, photosynthetic CO_2 assimilation and xanthophyll cycle interconversions during dehydration in desiccation-tolerant and intolerant liverworts. Planta 207: 224-228.

Dilks, T. J. K. and Proctor, M. C. F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. J. Bryol. 8: 317-336.

Dilks, T. J. K. and Proctor, M. C. F. 1976a. Seasonal variation in desiccation tolerance in some British bryophytes. J. Bryol. 9: 239-247.

Dilks, T. J. K. and Proctor, M. C. F. 1976b. Effects of intermittent desiccation on bryophytes. J. Bryol. 9: 249-264.

Dilks, T. J. K. and Proctor, M. C. F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol. 82: 97-114.

Duckett, J. G. and Pressel, S. 2003. Studies of protonemal morphogenesis in mosses. IX. *Discelium nudum*, exquisite pioneer of unstable clay banks. J. Bryol. 25: 241-246.

During, H. J. 1979. Life strategies of Bryophytes: A preliminary review. Lindbergia 5: 2-18.

During, H. J. 1992. Ecological classifications of bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). Bryophytes and Lichens in a Changing Environment, Clarendon Press, Oxford, pp. 1-31.

Egunyomi, A. 1979. Autecology of *Octoblepharum albidum* Hedw. in W. Nigeria II. Phenology and water relations. Nova Hedw. 31: 377-389.

El-Saadawi, W. and Zanaty, M. S. 1990. *Bryum bicolor* Dicks. and *Funaria hygrometrica* Hedw. develop remarkable persisting structures in extreme environment. J. Hattori Bot. Lab. 68: 285-291.

Erxleben, A., Gessler, A., Vervliet-Scheebaum, M., and Reski, R. 2012. Metabolite profiling of the moss *Physcomitrella patens* reveals evolutionary conservation of osmoprotective substances. *Plant Cell Repts.* 31: 427-436.

Fisher, K. M. 2008. Bayesian reconstruction of ancestral expression of the LEA gene families reveals propagule-derived desiccation tolerance in resurrection plants. Amer. J. Bot. 95: 506-515.

Green, T. G. A., Sancho, L. G., and Pintado, A. 2011. Ecophysiology of desiccation/rehydration cycles in mosses and lichens. In: Lüttge, U., Beck, E., and Bartels, D. (eds.). Plant Desiccation Tolerance. Springer-Verlag, Berlin, pp. 89-120.

Grusak, M. A., Thomas, R. J., and Marsh, B. H. 1980. Wall regeneration by plasmolysed cells from tissue suspension cultures of *Sphaerocarpos donnellii*. J. Cell Sci. 43: 167-175.

Gupta, R. K. 1976. The physiology of the desiccation resistance in bryophytes: Nature of organic compounds leaked from desiccated liverwort, *Plagiochila asplenioides*. Biochem. Physiol. Pflanz. 170: 389-395.

Gupta, R. K. 1977. A study of photosynthesis and leakage of solutes in relation to the desiccation effects in bryophytes. Can. J. Bot. 55: 1186-1194.

Gupta, R. K. 1979. Leakage of photosynthates from water-stressed liverwort *Scapania undulata* (L.) Dum. Indian J. Exper. Biol. 17: 164-166.

Guschina, I. A., Harwood, J. L., Smith, M., Beckett, R. P. 2002. Abscisic acid modifies the changes in lipids brought about by water stress in the moss *Atrichum androgynum*. New Phytol. 156: 255-264.

Hájek, T. and Beckett, R. P. 2008. Effect of water content components on desiccation and recovery in *Sphagnum* mosses. Ann. Bot. 101: 165-173.

Hájek, T. and Vicherová, E. 2014. Desiccation tolerance of *Sphagnum* revisited: A puzzle resolved. Plant Biol. 16: 765-773.

Hamerlynck, E. P., Csintalan, Z., Nagy, Z., Tuba, Z., Goodin, D., and Henebry, G. M. 2002. Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss *Tortula ruralis*. Oecologia 131: 498-505.

He, X., Sun, Y., and Zhu, R. L. 2013. The oil bodies of liverworts: Unique and important organelles in land plants. Crit. Rev. Plant Sci. 32: 293-302.

Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Lehre, Germany, 157 pp. + 80 Plates.

Heber, U., Bukhov, N. G., Shuvalov, V. A., Kobayashi, Y., and Lange, O. L. 2001. Protection of the photosynthetic apparatus against damage by excessive illumination in homoiohydric leaves and poikilohydric mosses and lichens. J. Exper. Bot. 52: 1999-2006.

Hedderson, T. A. and Longton, R. E. 1996. Life history variation in mosses: Water relations, size and phylogeny. Oikos 77: 31-43.

Hellwege, E. M., Dietz, K.-J., Volk, O. H., and Hartung, W. 1994. Abscisic acid and the induction of desiccation tolerance in the extremely xerophilic liverwort *Exormotheca holstii*. Planta 194: 525-531.

Henckel, P. A. and Pronina, N. D. 1968. Factors underlying dehydration resistance in poikiloxerophytes. Sov. Plant Physiol. 15: 68-74.

Henckel, P. A. and Pronina, N. D. 1969. Anabiosis with desiccation of the poikiloxerophytic flowering plant *Myrothamnus flabellifolia*. Sov. Plant Physiol. 16: 745-749.

Henckel, P. A. and Pronina, N. D. 1973. The euxerophytic affiliation of *Haberlea rhodopensis* (Family Gesneriaceae). Sov. Plant Physiol. 20: 690-692.

Hernández-Garcia, C. D., González-Mancebo, J. M., and Losada-Lima, A. 1999. Water relations of some mosses growing in pine forests of Tenerife, Canary Islands. Lindbergia 24: 15-22.

Hoekstra, F. A. 2005. Differential longevities in desiccated anhydrobiotic plant systems. Integrat. Compar. Biol. 45: 725–733.

Iljin, W. S. 1953. Causes of death of plants as a consequence of loss of water: Conservation of life in desiccated tissues. Bull. Torrey Bot. Club 80: 166-167.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8; 257-274.

James, T. A. 1981. Stable carbon isotope analysis of mosses and lichens growing in xeric and moist habitat. Bryologist 84: 79-81.

Johnsen, A. B. 1969. Phenological and environmental observations on stands of *Orthotrichum anomalum*. Bryologist 72: 397-403

Kappen, L. and Valladares, F. 1999. Opportunistic growth and desiccation tolerance: The ecological success of poikilohydrous autotrophs. In: Pugnaire, F. I. and Valladares, F. (eds.). Handbook of Functional Plant Ecology. Marcel Dekker, New York, pp. 121-194.

Kis, G. and Pócs, T. 1997. Oil body studies on African Hepaticae. J. Hattori Bot. Lab. 81: 175-242.

Koster, K. L., Balsamo, R. A., Espinoza, C., and Oliver, M. J. 2010. Desiccation sensitivity and tolerance in the moss *Physcomitrella patens*: Assessing limits and damage. Plant Growth Reg. 62: 293-302.

Kozlowski, A. 1921. Sur l'origine des ol´eoleucites chez les h´epatiques `a leuilles. C. R. Acad. Sci. Paris 173: 497-499.

Krochko, J. E., Bewley, J. D., and Pacey, J. 1978. The effects of rapid and very slow speeds of drying on the ultrastructure and metabolism of the desiccation-sensitive moss *Cratoneuron filicinum* (Hedw.) Spruce. J. Exper. Bot. 29: 905-917.

Kronestedt, E. 1983. Cytology of oil-body cells in *Ricciocarpus natans*. Nordic J. Bot. 35: 547-558.

Larcher, W. 1983. Physiological Plant Ecology. Trans. by M. A. Biederman-Thorson. Springer-Verlag, Berlin, 303 pp.

Lee, J. A. and Stewart, G. R. 1971. Desiccation injury in mosses. I. Intraspecific differences in the effect of moisture stress on photosynthesis. New Phytol. 70: 1061-1068.

Li, Y., Glime, J. M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. J. Bryol. 17: 59-70.

Li, Z.-Y., Tian, X.-R., Chen, J., and Li, J. 2009. Physiological response of *Plagiomnium acutum* during desiccation and rehydration process. Guihaia 29: 139-142.

Maheu, J. 1902. Regeneration du *Barbula muralis* apres 14 ans de secheresse par protonemas foliaires primaires propaguliferes et protonemas secondaires bulbigenes. Bull. Soc. Bot. France, Colloque Bryol. 69: 330-334.

Malta, N. 1921. Versuche über die Widerstandsfähigkeit der Moose gegen Austrocknung. Acta Univ. Latviensis 1: 125-129.

Mankiewicz, P. S. 1983. Water conduction by external capillary spaces and the shape of bryophyte colonies. Amer. J. Bot. 70 (5 Part 2): 5-6.

Mankiewicz, P. S. 1984a. The adaptive geometry of bryophyte colonies: Some limits to size, shape, and branching strategy set by the surface tension of water. Amer. J. Bot. (Abstr. Suppl.) 71(5 part 2): 82.

Mankiewicz, P. S. 1984b. External capillary conduction of water in bryophyte colonies: Some limits to size, shape and branching strategy set by the surface tension of water. Amer. J. Bot. (Abstr. Suppl.) 71 (5 Part 2): 82.

Mankiewicz, P. S. 1987a. Bryophyte colony growth-forms: A new perspective based on the geometry of water potential and microhabitat. Amer. J. Bot. 74: 598.

Mankiewicz, P. S. 1987b. The low pressure field porometer: A new, low cost technique for characterizing external capillary water conduction in whole colonies of bryophytes and other small plants. Bryologist 90: 253-262.

Mizushima, U. 1980. Water relations in *Entodon rubicundis* (Mitt.) Jaeg. Proc. Bryol. Soc. Japan 2(9): 124-126.

Moore, C. J., Luff, S. E., and Hallam, N. D. 1982. Fine structure and physiology of the desiccation-tolerant mosses, *Barbula torquata* Tayl. and *Triquetrella papillata* (Hook. F. and Wils.) Broth., during desiccation and rehydration. Bot. Gaz. 143: 358-367.

Mägdefrau, K. 1935. Untersuchungen über die Wasserversorgung des Gametophyten und Sporophyten der Laubmoose. Zeitschr. Bot. 29: 337-375.

Nagao, M., Minami, A., Arakawa, K., Fujikawa, S., and Takezawa, D. 2005. Rapid degradation of starch in chloroplasts and concomitant accumulation of soluble sugars associated with ABA-induced freezing tolerance in the moss *Physcomitrella patens*. J. Plant Physiol. 162: 169-180.

Nichols, G. E. 1918. War work for bryophytes. Bryologist 21: 53-56.

Noailles, M. 1978. Etude ultrastructurale de la récupération hydrique aprè une période de sècheresse chez une hypnobryale: *Pleurozium schreberi* (Willd.) Mitt. Ann. Sci. Nat. Bot. Paris 12e Ser. 19(4): 249-265.

Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. Bot. J. Linn. Soc. 104: 281-291.

Ochi, H. 1952. The preliminary report on the osmotic value, permeability, drought and cold resistance of mosses. Bot. Mag. Tokyo 65: 763-764.

Oldenhof, H., Wolkers, W. F., Bowman, J. L., Tablin, F., and Crowe, J. H. 2006. Freezing and desiccation tolerance in the moss *Physcomitrella patens*: An *in situ* Fourier transform infrared spectroscopic study. Biochim. Biophys. Acta 1760: 1226-1234.

Oliver, M. J. and Bewley, J. D. 1984. Desiccation and ultrastructure in bryophytes. Advances Bryol. 2: 91-131.

Oliver, M. J., Mishler, B. D., and Quisenberry, J. E. 1993. Comparative measures of desiccation-tolerance in the *Tortula ruralis* complex. I. Variation in damage control and repair. Amer. J. Bot. 80: 127-136.

Oliver, M. J., Wood, A. J., and O'Mahony, P. 1998. "To dryness and beyond" – preparation for the dried state and rehydration in vegetative desiccation-tolerant plants. Plant Growth Reg. 24: 193-201.

Oliver, M. J., Tuba, Z., and Mishler, B. D. 2000. The evolution of vegetative desiccation tolerance in land plants. Plant Ecol. 151: 85-100.

Oliver, M. J., Dowd, S. E., Zaragoza, J., Mauget, S. A., and Payton, P. R. 2004. The rehydration transcriptome of the desiccation-tolerant bryophyte *Tortula ruralis*: Transcript classification and analysis. Bmc Genomics 5(1): 89.

Oliver, M. J., Velten, J., and Mishler, B. D. 2005. Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats. Integr. Compar. Biol. 45: 788-799.

Peintinger, M. 1988. Die Vegetation des Litzelsees bei Markelfingen (Westliches Bodenseegebiet). Carolinea 46: 17-22.

Pence, V. C. 1998. Cryopreservation of bryophytes: The effects of abscisic acid and encapsulation dehydration. Bryologist 101: 278-281.

Pigòn, A. and Weglarska, B. 1955a. Rate of metabolism in tardigrades during active life and anabiosis. Nature 176: 121-122.

Pigòn, A. and Weglarska, B. 1955b. Anabiosis in Tardigrada: Metabolism and humidity. Acad. Pol. Sci. Bull., Ch. II, 3: 31-34.

Pressel, S., Duckett, J. G., Ligrone, R., and Proctor, M. C. F. 2009. Effects of de- and rehydration in desiccation-tolerant liverworts: A cytological and physiological study. Internat. J. Plant Sci. 170: 182-199.

Price, J. S. 1991. Evaporation from a blanket bog in a foggy coastal environment. Boundary-layer Meteorol. 57: 391-406.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. In: International Symposium on Bryophyte Ecology, Edinburgh, UK. J. Linn. Soc. Bot. 104: 61-77.

Proctor, M. C. F. 1999. Water-relations parameters of some bryophytes evaluated by thermocouple psychrometry. J. Bryol. 21: 263-270.

Proctor, M. C. F. 2000. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Proctor, M. C. F. 2001. Patterns of desiccation tolerance and recovery in bryophytes. Plant Growth Reg. 35(2): 147-156.

Proctor, M. C. F. 2004. How long must a desiccation-tolerant moss tolerate desiccation? Some results of two years' data logging on *Grimmia pulvinata*. Physiol. Plant. 122: 21-27.

Proctor, M. C. F. 2010. Recovery rates of chlorophyll-fluorescence parameters in desiccation-tolerant plants: Fitted logistic curves as a versatile and robust source of comparative data. Plant Growth Reg. 62: 233-240.

Proctor, M. C. F. 2014. The diversification of bryophytes and vascular plants in evolving terrestrial environments. In: Hanson, D. T. and Rice, S. K. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Advances in Photosynthesis and Respiration 37: 59-77.

Proctor, M. C. R., Nagy, Z., Csintalan, Z., and Takács, Z. 1998. Water-content components in bryophytes: analysis of pressure-volume relationships. J. Exper. Bot. 1845-1854.

Proctor, M. C. F., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., and Mishler, B. D. 2007. Desiccation-tolerance in bryophytes: A review. Bryologist 110: 595-621.

Raven, J. A. 1999. The size of cells and organisms in relation to the evolution of embryophytes. Plant Biol. 1(1): 2-12.

Renault, S., Bonnemain, J. L., Faye, L., and Gaudillere, J. P. 1992. Physiological aspects of sugar exchange between the gametophyte and the sporophyte of *Polytrichum formosum*. Plant Physiol. 100: 1815-1822.

Richardson, D. H. S. 1981. The Biology of Mosses. John Wiley & Sons, Inc., N. Y., 220 pp.

Risse, S. 1993. Very large tubers in *Bryum bicolor* Dicks. J. Bryol. 17: 505-509.

Rundel, P. W., Stichler, W., Zander, R. H., and Ziegler, H. 1979. Carbon and hydrogen isotope ratios of bryophytes from arid and humid regions. Oecologia (Berlin) 44: 91-94.

Rushing, A. E. and Anderson, W. B. 1996. The sporophyte-gametophyte junction in the moss *Acaulon muticum* (Pottiaceae): Early stages of development. Amer. J. Bot. 83: 1274-1281.

Russell, S. 1982. Humidity gradients and bryophyte zonation in the Afromontane forests of the eastern Cape, South Africa. J. Hattori Bot. Lab. 52: 299-302.

Sagot, C. and Rochefort, L. 1996. Tolerance des Sphaignes a la desiccation. [Tolerance of *Sphagnum* to desiccation.]. Cryptog. Bryol. Lichénol. 17: 171-183.

Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140: 677-684.

Schroeter, B., Sancho, L. G., and Valladares, F. 1999. In situ comparison of daily photosynthetic activity patterns of saxicolous lichens and mosses in Sierra de Guadarrama, central Spain. Bryologist 102: 623-633.

Seel, W. E., Baker, N. R., and Lee, J. A. 1992. Analysis of the decrease in photosynthesis on desiccation of mosses from xeric and humid environments. Physiol. Plant. 86: 451-458.

Silvola, J. 1991. Moisture dependence of CO_2 exchange and its recovery after drying in certain boreal forest and peat mosses. Lindbergia 17: 5-10.

Simon, E. W. 1974. Phospholipids and plant membrane permeability. New Phytol. 73: 377-420.

Simon, E. W. 1978. Membranes in dry and imbibing seeds. In: Crowe, J. H. and Clegg, J. S. (eds.). Dry Biological Systems. Academic Press, New York, London, pp. 205-224.

Šinžar-Sekulić, J., Sabovljević, M., and Stevanović, B. 2005. Poređenje tolerancije isušivanja kod mahovina sa različitih staništa. [Comparison of desiccation tolerance among mosses from different habitats.]. Arch. Biol. Sci. (Belgrade) 57: 189-192.

Skré, O., Oechel, W. C., and Miller, P. M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can. J. Forest. Res. 13: 860-868.

Smith, R. L. 1986. Elements of Ecology. Harper & Row, Publ., New York, 677 pp.

Sollows, M. C., Frego, K. A., and Norfolk, C. 2001. Recovery of *Bazzania trilobata* following desiccation. Bryologist 104: 421-429.

Stark, L. R. and Brinda, J. C. 2015. Developing sporophytes transition from an inducible to a constitutive ecological strategy of desiccation tolerance in the moss *Aloina ambigua*: Effects of desiccation on fitness. Ann. Bot.115: 593-603.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2013. The desert moss *Pterygoneurum lamellatum* (Pottiaceae) exhibits an inducible ecological strategy of desiccation tolerance: Effects of rate of drying on shoot damage and regeneration. Amer. J. Bot. 100: 1522-1531.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2014. Physiological history may mask the inherent inducible desiccation tolerance strategy of the desert moss *Crossidium crassinerve*. Plant Biol. 16: 935-946.

Toldi, O., Tuba, Z., and Scott, P. 2009. Vegetative desiccation tolerance: Is it a goldmine for bioengineering crops? Plant Sci. 176: 187-199.

Tuba, Z. 1984. Changes in the photosynthetic pigment system of the drought tolerant *Tortula ruralis* during daily desiccation. In: Vana, J. (ed.). Proceedings of the Third Meeting of Bryologists from Central and East Europe, Univerzita Karlova, Praha, pp. 343-352.

Tuba, Z. 1985. Photosynthetic pigment responses in *Tortula ruralis* during daily desiccation. Abstr. Bot. 9, Suppl. 2: 231-239.

Tucker, E. B., Costerton, J. W., and Bewley, J. D. 1975. The ultrastructure of the moss *Tortula ruralis* on recovery from desiccation. Can. J. Bot. 53: 94-101.

Volk, O. H. 1984. Beiträge zur Kenntnis der Marchantiales in Suedwest-Afrika/Namibia. IV. Zur Biologie einiger Hepaticae mit besonderer Beruecksichtigung der Gattung *Riccia*. [Contribution to the knowledge of the Marchantiales in Southwest Africa/Namibia. IV. The biology of some Hepaticae with particular consideration of the genus *Riccia*.]. Nova Hedw. 39: 117-144.

Wagner, D. J. and Titus, J. E. 1984. Comparative desiccation tolerance of two *Sphagnum* mosses. Oecologia 62: 182-187.

Wang, X. Q., Yang, P. F., Liu, Z., Liu, W. Z., Hu, Y., Chen, H., Kuang, T. Y., Pei, Z. M., Shen, S. H., and He, Y. K. 2009. Exploring the mechanism of *Physcomitrella patens* desiccation tolerance through a proteomic strategy. Plant Physiol. 149: 1739-1750.

Watkins, J. E. Jr., Mack, M. C., Sinclair, T. R., and Mulkey, S. S. 2007. Ecological and evolutionary consequences of desiccation tolerance in tropical fern gametophytes. New Phytologist 176: 708-717.

Werner, O., Ros Espín, R. M., Bopp, M., and Atzorn, R. 1991. Abscisic acid-induced drought tolerance in *Funaria hygrometrica* Hedw. Planta 186: 99-103.

Williams, T. G. and Flanagan, L. B. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*. Oecologia 108: 38-46.

Wolkers, W. F., McCready, S., Brandt, W. F., Lindsey, G. G., and Hoekstra, F. A. 2001. Isolation and characterization of a D-7 LEA protein from pollen that stabilizes glasses in vitro. Bba-Protein Struc. Molec. Enzymol.1544: 196-206.

Wood, A. J. 2007. Frontiers in bryological and lichenological research. The nature and distribution of vegetative desiccation tolerance in hornworts, liverworts and mosses. Bryologist 110: 163-167.

Wu, N., Zhang, Y. M., Downing, A., Zhang, J., and Yang, C. 2012. Membrane stability of the desert moss *Syntrichia caninervis* Mitt. during desiccation and rehydration. J. Bryol. 34: 1-8.

Xu, J., Bai, X. L., Tian, G. Q., Yao, Y. P., and Gao, T. Y. 2005. Study on moss: The content of amino acid, the feature of nutritive elements and its resistance to drought in the biotic crusts in arid and semi-arid regions. *Acta Ecol. Sinica* 25: 1247-1255.

Yang, H. L., Zhang, D. Y., Wang, J. C., Wood, A. J., and Zhang, Y. M. 2012. Molecular cloning of a stress-responsive aldehyde dehydrogenase gene ScALDH21 from the desiccation-tolerant moss *Syntrichia caninervis* and its responses to different stresses. Molec. Biol. Repts. 39: 2645-2652.

Zacherl, H. 1956. Physiologische und Okologische Untersuchungen über die innere Wasserleitung bei Laubmoosen. Z. Bot. 44: 409-436.

Zhang, J., Zhang, Y.-M., Downing, A., Wu, N., and Zhang, B.-C. 2011. Photosynthetic and cytological recovery on remoistening *Syntrichia caninervis* Mitt., a desiccation-tolerant moss from Northwestern China. Photosynthetica 49: 13-20.

CHAPTER 7-6

WATER RELATIONS: REHYDRATION AND REPAIR

TABLE OF CONTENTS

Uniqueness of Bryophytes 7-6-2
Duration survival 7-6-4
Resumption of Activity 7-6-4
    Leakage and Membrane Repair 7-6-10
    Protein Degradation and Ubiquitin 7-6-12
    Respiration 7-6-12
    Reactive Oxygen Species 7-6-12
    Photosynthesis 7-6-12
Architectural Changes 7-6-14
    Cellular Changes 7-6-15
    Leptoid Recovery 7-6-16
    Chloroplast Recovery 7-6-15
    Photodamage 7-6-16
    Measuring Damage 7-6-17
Factors Affecting Recovery 7-6-17
    Temperature 7-6-17
    Drying Speed 7-6-17
    Frequency of Dehydration/Rehydration 7-6-18
Carbon Balance 7-6-19
Implications 7-6-20
Summary 7-6-20
Acknowledgments 7-6-20
Literature Cited 7-6-20

CHAPTER 7-6

WATER RELATIONS: REHYDRATION AND REPAIR

Figure 1. ***Palustriella commutata*** rehydrating in the spring runoff. Photo by Michael Lüth, with permission.

Uniqueness of Bryophytes

As Vitt *et al*. (2014) stated, desiccation tolerance is the ability to survive complete loss of free water, a trait found in many bryophytes. One striking difference between bryophytes and tracheophytes is that if you put a dry bryophyte into water, in most cases you will see an immediate change in turgor, and leaves will spread and take their normal hydrated position – one that presents the greatest surface area to the light and atmospheric CO_2. This is particularly striking in mosses from frequently dry habitats, such as ***Hedwigia ciliata*** (Figure 2) from rocks or ***Syntrichia ruralis*** (Figure 3, Figure 21) from open sand. In many mosses, such as ***Polytrichum*** s.l. (Figure 8, Figure 10) and ***Syntrichia***, this ability to spread the leaves when moist and appress them to the stem when dry is the result of enlarged or hyaline leaf base cells (Figure 4) that absorb water easily and swell, forcing the leaf away from the stem.

Figure 2. ***Hedwigia ciliata*** growing on rock. Photo by Janice Glime.

Figure 3. ***Syntrichia ruralis*** on sand dunes at Harlech, Wales. Photo by Janice Glime.

Figure 4. ***Brachythecium rivulare*** decurrent leaf base with enlarged hyaline cells at leaf base. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Bryophytes can look dead, but come back to life when rehydrated. For example, Longton and Schuster (1983) noted that both ***Pleurozium schreberi*** (Figure 5) and ***Bryum argenteum*** (Figure 6) can have dark or moribund lower shoot tissues, but new shoots and protonemata can regenerate from them. Clymo and Duckett (1986) made similar observations on ***Sphagnum***.

Figure 5. ***Pleurozium schreberi*** with moribund lower shoot tissues exposed. Photo by Janice Glime.

Figure 6. ***Bryum argenteum*** showing the moribund lower leaves. Photo from Botany Website, UBC, with permission.

Figure 7. ***Sphagnum girgensohnii***. Note the change in color in lower branches, indicating senescing conditions. Photo by Bernd Haynold through Wikimedia Commons.

Rehydration in mosses is generally very rapid, but some taxa are rather recalcitrant about getting wet inside. ***Polytrichum piliferum*** (Figure 8), common on sand in dry, exposed habitats, and ***Schistidium apocarpum*** (Figure 9), a rock-dweller, can require two hours to become saturated, whereas ***Polytrichum juniperinum*** (Figure 10), a soil moss with wider ecological amplitude than ***P. piliferum***, can become saturated within three minutes (Larson 1981). Larson points out that the surface area to mass ratio is very important in determining the speed of rewetting (Figure 11). The **cuticle** seems to be another contributing factor in mosses like **Polytrichaceae** and **Mniaceae**.

Figure 8. ***Polytrichum piliferum*** in hydrated state. Photo by Janice Glime.

Figure 9. ***Schistidium apocarpum*** in its dry state with leaves wrapped around stem. Photo by Michael Lüth, with permission.

Figure 10. ***Polytrichum juniperinum*** in hydrated state. Photo by Janice Glime.

Duration Survival

Determining the length of time that bryophytes can survive desiccation can be tricky. Although use of herbarium specimens can provide starting dates, these are stored in the dark, which may differ considerably from survival in the light where chlorophyll can be damaged. And one can never be sure how often the moss was wet for examination, often using up resources for repair without having an opportunity to replace them before being put in the dark again and once again desiccated.

Studies to test viability directly after an assortment of desiccation times are rare, requiring careful record keeping and assurance the conditions remain relatively constant over a lengthy period of time. Specimens must then be rehydrated at intervals, requiring multiple specimens and replication, all collected at the same time from one location.

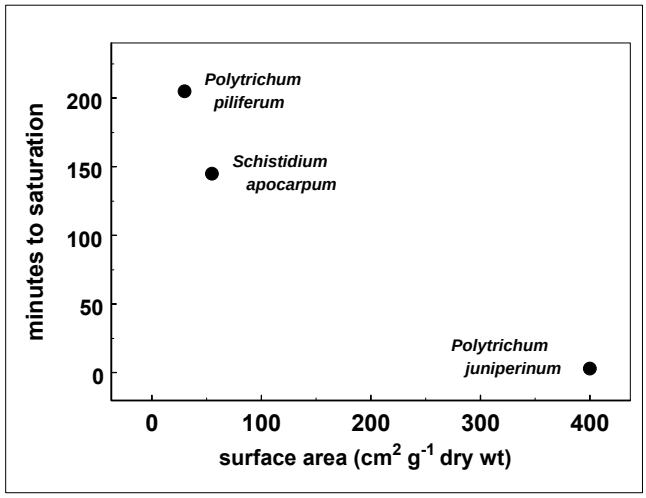

Figure 11. Relationship between surface area and time to saturation upon rewetting of three drought-tolerant mosses. Based on Larson (1981).

Ochi (1952) reminds us that even season of collection will affect the degree to which bryophytes can survive desiccation and the length of time they can remain dry and survive, an interpretation reiterated by Kosokawa and Kubota (1957). For example, Dilks and Proctor (1976b) commented that British species of bryophytes tend to have an increased tolerance to drought in spring and summer.

Hoekstra (2005) concluded that small size was not a limiting factor in desiccation survival longevity. Factors such as membrane deterioration during desiccation affect the length of time an organism can survive the desiccation (Koster *et al*. 2010). Hoekstra (2005) likewise attributed survival to a high level of fatty acid saturation in membranes.

Longevities vary considerably among plants, ranging from a few days in some pollen to decades in some moss spores and even green moss tissue (Hoekstra 2005). In 2000, Alpert (2000) asserted that "some desiccation-tolerant species can survive without water for over ten years." Alpert cited duration periods of adult organisms as 34 years for fungi, 23 years for liverworts, 19 years for mosses, 5 years for ferns and angiosperms, and 1 year for lichens. Hornwort spores can tolerate 21 years of desiccation (Vanderpoorten & Goffinet 2009). Some bryophytes exceed these duration records (Table 1).

Even within a fen, desiccation tolerance can vary widely. When eight fen species were compared, it was the hummock moss species ***Climacium dendroides*** (Figure 12), ***Aulacomnium palustre*** (Figure 13), and ***Tomentypnum nitens*** (Figure 14) that had the highest desiccation survival (>10% of stems after 20 weeks of desiccation). ***Hamatocaulis vernicosus*** (Figure 15), ***Calliergonella cuspidata*** (Figure 16), and ***Bryum pseudotriquetrum*** (Figure 17) had moderate resilience (<10% stem survival after 12 weeks). The lowest survival rates occurred in ***Campylium stellatum*** (Figure 18) and ***Plagiomnium elatum*** (Figure 19) (~0% survival after 6 weeks).

Figure 12. ***Climacium dendroides***, a hummock species with high desiccation survival. Photo by Michael Lüth, with permission.

Figure 13. ***Aulacomnium palustre***, a species that has high desiccation tolerance on hummock tops. Photo by Michael Lüth, with permission.

Figure 14. ***Tomentypnum nitens***, a species with high desiccation tolerance on hummocks. Photo by Michael Lüth, with permission.

Figure 15. ***Hamatocaulis vernicosus***, a species with moderate resilience to desiccation. Photo by Michael Lüth, with permission.

Figure 16. ***Calliergonella cuspidata***, a species with moderate resilience to desiccation. Photo by Michael Lüth, with permission.

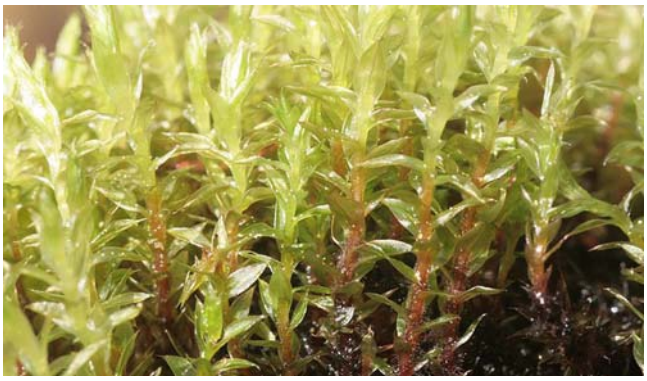

Figure 17. ***Bryum pseudotriquetrum***, a species with moderate resilience to desiccation. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Campylium stellatum***, a species with poor survival of desiccation. Photo by Michael Lüth, with permission.

Figure 19. ***Plagiomnium elatum***, a species with poor survival of desiccation. Photo by Michael Lüth, with permission.

Table 1. Bryophytes and known desiccation survival times. Based mostly on Stark *et al*. 2016.

Species	Duration Dry	Reference
Mosses		
Andreaea rothii	13 mos	Proctor 1981
Anisothecium staphylinum	45-48 yr (spores, tubers, or rhizoids in dry soil)	Whitehead 1984
Anoectangium compactum	19 yr	Malta 1921
Anomodon longifolius	2 yr	Richardson 1981
Anomodon viticulosus	45 d	Hinshiri & Proctor 1971
Archidium ohioense	20 yr [4]	Makinde & Fajuke 2009
Barbula torquata	18 mos	Moore *et al*., 1982
Bryum argenteum	2 yr	Richardson 1981
Bryum coronatum	20 yr [4]	Makinde & Fajuke 2009
Dicranella heteromalla	0 d [1]	Streusand & Ikuma 1986
Dicranoweisia cirrata	9 yr	Richardson 1981
Fissidens minutifolius	6 yr [4]	Makinde 1993
Fissidens subglaucissimus	20 yr [4]	Makinde & Fajuke 2009
Fissidens taxifolius	0 d [1]	Streusand & Ikuma 1986
Fontinalis flaccida	3 mos	Glime 2015
Grimmia apocarpa	8 mos	Alpert & Oechel 1987
Grimmia laevigata	10 mos; 10 yr (shoots), 1 mo (protonema)	Alpert & Oechel 1985; Breuil-Sée 1994; Keever, 1957
Grimmia muehlenbeckii	1.5 yr	Richardson 1981
Grimmia pulvinata	<7 yr	Segreto *et al*. 2010
Grimmia elatior	5 yr	Richardson 1981
Grimmia torquata	<7 yr	Segreto *et al*. 2010
Hookeria lucens	~15 d	Dilks & Proctor 1974
Hylocomium splendens	~160 d	Dilks & Proctor 1974
Neckera crispa	~160 d	Dilks & Proctor 1974
Octoblepharum albidum	29 wk (leaves); 20 yr [4]	Egunyomi 1979; Makinde & Fajuke 2009
Orthotrichum rupestre	9 mos; ~2 yr	Alpert & Oechel 1987; Richardson 1981
Plagiothecium undulatum	100 d	Dilks & Proctor 1974
Racomitrium lanuginosum	>239 d	Dilks & Proctor 1974
Rhytidiadelphus loreus	>100 d	Dilks & Proctor 1974
Scorpiurium circinatum	~120 d	Dilks & Proctor 1974
Sphagnum fallax	14 d	Sagot & Rochefort 1996
Sphagnum fuscum	14 d; 0 d [2]	Sagot & Rochefort 1996; Schipperges & Rydin 1998
Sphagnum magellanicum	14 d; 0 d [2]	Sagot & Rochefort 1996; Schipperges & Rydin 1998
Sphagnum [3 spp.]	0 d [2]	Schipperges & Rydin 1998
Syntrichia caninervis	3 yr; 6 yr	Oliver *et al*. 1993; Oliver *et al*. 2005
Syntrichia norvegica	3 yr	Oliver *et al*. 1993
Syntrichia ruralis	3 yr; 14 yr	Oliver *et al*. 1993; Maheu 1922; Stark *et al*. 2016
Tortula muralis	3 yr; 14 yr	Kosnar & Kolar 2009; Glime 2015
Triquetrella papillata	8 wk	Moore *et al*. 1982
13 Antarctic species	<1 yr	Davey 1997
8 fen spp.	8–20 wk	Manukjanová *et al*. 2014
protonemal resting cells	49 yr	Bristol 1916
Liverworts		
Bazzania trilobata	0 d	Sollows *et al*., 2001
Marchantia berteroana	<1 yr	Davey 1997
Oxymitra paleacea	4 yr	Volk 1984
Plagiochila spinulosa	~30 d	Dilks & Proctor 1974
Reboulia hemisphaerica	4 yr	Volk 1984
Riccia canescens	7 yr	Volk 1984
Riccia macrocarpa	23 yr	Breuil-Sée 1993
Riccia macrospora	2 yr	Volk 1984
Riccia marginata	2 yr	Volk 1984
Saccogyna viticulosa	~200 d	Dilks & Proctor 1974
13 species of hepatics [3]	≤20 mos	Volk 1984

[1] shoots allowed to regenerate only 10–14 d

[2] 13 species of *Sphagnum* were shown capable of hardening to DT when partially desiccated at high RHs (Hájek & Vicherová, 2014)

[3] in the genera *Corsinia*, *Mannia*, *Plagiochasma*, and *Riccia*

[4] based on visible presence of neutral red stain in vacuoles upon rehydration

The duration of desiccation that plants can survive is dependent on the antioxidant pool present at the time of desiccation (Kranner *et al*. 2002; Moore *et al*. 2009). This is because longer periods of desiccation result in greater oxidative damage.

Certain events must occur upon rehydration for the bryophyte to survive (Pressel & Duckett 2010). Using moss protonemata, they determined that cell death will occur if these events do not occur. Slow drying will usually prevent these cell death threats.

This raises the question of desiccation survival under desert conditions, where drying can be quite rapid. For leaves, development will be interrupted, but they seem able to resume (Stark 2005). On the other hand, when sporophyte development is interrupted frequently, the sporophyte seems to fail, with only 9 out of 248 surviving during the 4-year study period. Embryonic abortion accounted for 69% of these, whereas 30% was attributable to herbivory. In the Mojave Desert moss ***Crossidium crassinerve*** (Figure 20) required a rain event of at least 2 mm to fully rehydrate. In most cases, the only useful hydration periods occurred in the cooler months of October to April, with a mean hydroperiod of 3.7-4.9 days. Although most dry periods were less than 25 days, Stark recorded them as long as 191 days. In a late winter rain event, the moss patches dried slowly over a period of several days, but during a summer event, the patches were dry in as few as 3 hours.

Figure 20. ***Crossidium crassinerve***, a species in the Mojave Desert where it requires at least 2 mm of rain to fully rehydrate. Photo by Jan-Peter Frahm, with permission.

Resumption of Activity

Upon rehydration, desiccation-tolerant bryophytes generally resume normal activity quickly (Csintalan *et al*. 1999), whereas the resurrection plants among the tracheophytes in the same habitat take much longer (Peterson *et al*. 1994; Marschall & Proctor 1999).

Using the moss ***Anomodon viticulosus*** (Figure 37) and leafy liverwort ***Porella platyphylla*** (Figure 23), both from habitats that dry out frequently, Hinshiri and Proctor (1971) found a consistent pattern of net assimilation upon rehydration. When desiccated up to 22 days at 50% relative humidity in ***Anomodon viticulosus*** (Figure 37) and 60 days in ***Porella platyphylla*** (Figure 23), the plants recovered in 3-4 hours. However, after longer periods, the initial net assimilation was negative, progressively becoming positive during the next several days. After 70 days, respiration in ***Anomodon viticulosus*** is very high in the first 24 hours of rehydration, then drops to normal levels. However, even then recovery is not assured. This negative initial net assimilation explains why frequent desiccation with short periods in which to recover before the next one is usually lethal to the bryophytes. In ***Polytrichastrum formosum*** (Figure 28), full recovery requires 24 hours (Duckett *et al*. 2007).

There are two general strategies that permit drought-tolerant plants to survive periods of desiccation: cellular protection and cellular repair. Those bryophytes that are tolerant of desiccation seem to succeed primarily because of their rapid cellular repair (Oliver *et al.* 1993). According to Oliver (1991), no novel **mRNA**s (messenger RNA; molecule that carries portion of DNA code to other parts of the cell processing) are recruited or favored for translation during desiccation. Rather, in ***Syntrichia ruralis*** (Figure 21), there is a loss of 25 **hydration** proteins (those present in a normal hydrated state), whereas 74 **rehydration** proteins are synthesized upon rehydration. This system, rather than protecting the moss from desiccation as in most tracheophytes, prepares bryophytes for repair. This is probably essential because their one-cell-thick leaves remain at full turgor, carrying out photosynthesis, then become desiccated very rapidly before going into a state of water stress and suspended metabolism (Proctor 2000b).

Figure 21. ***Syntrichia ruralis***, a moss that loses hydration proteins upon drying and synthesizes rehydration proteins upon rewetting. Photo by Michael Lüth, with permission.

Antarctic mosses can suffer severe desiccation for prolonged periods. Rod Seppelt (Bryonet 2007) relates a story of an Antarctic ***Grimmia*** (Figure 22). A student had made a number of attempts at sectioning the dried moss without success. Seppelt suggested wetting the moss first and was amazed to discover, upon examination, that the cells were perfectly intact. When he re-examined the mosses that had been sitting on the lab bench for 15 months, but had been rewet for the sectioning, they had sprouted new shoots!

Figure 22. ***Schistidium chrysoneurum*** (formerly *Grimmia antarctici*) in Antarctica. Photo by Sharon Robinson, through Creative Commons.

Deltoro *et al*. (1998a) compared recovery in seven desiccation-tolerant bryophytes [Figure 23: ***Hedwigia ciliata***, ***Hypnum cupressiforme***, ***Leucodon sciuroides***, ***Orthotrichum cupulatum***, ***Pleurochaete squarrosa***, ***Porella platyphylla*** (Figure 23), and ***Syntrichia ruralis*** (Figure 21)] with that of seven desiccation-intolerant bryophytes [Figure 24: ***Cinclidotus aquaticus***, ***Philonotis calcarea***, ***Lunularia cruciata***, ***Conocephalum conicum***, ***Platyhypnidium riparioides***; ***Barbula bolleana*** (Figure 25-Figure 26), ***Palustriella commutata*** (Figure 1, Figure 27),]. All seven desiccation-tolerant bryophytes experienced full recovery, with many cellular activities back to normal rates within two hours (Deltoro *et al*. 1998a; Marschall & Proctor 1999). However, those species from the hydric and mesic habitats, the desiccation-intolerant ones, were unable to restore their photochemical activity.

Figure 23. Examples of drought-tolerant bryophytes. **Left, top: *Hedwigia ciliata***, **Left, Middle: *Leucodon sciuroides***, **Left, bottom: *Pleurochaete squarrosa***, **Right, top: *Orthotrichum cupulatum***, **Right, middle: *Hypnum cupressiforme***, **Right bottom: *Porella platyphylla***. Photos by Michael Lüth, with permission.

Figure 24. Examples of desiccation-intolerant bryophytes. **Left, top:** ***Cinclidotus aquaticus***, **Left, middle:** ***Philonotis calcarea***, **Left, bottom:** ***Lunularia cruciata***, **Right, top:** ***Conocephalum conicum***, **Right, bottom:** ***Platyhypnidium riparioides***. Photos by Michael Lüth; ***Conocephalum conicum*** photo by Janice Glime.

Figure 25. ***Barbula bolleana*** in a seepage waterfall. Photo by Michael Lüth, with permission.

Figure 26. ***Barbula bolleana***, a desiccation-intolerant moss. Photo by Michael Lüth, with permission.

Figure 27. ***Palustriella commutata***, a desiccation-intolerant species. Photo by J. C. Schou, with permission.

Proctor *et al*. (2007) used ***Polytrichastrum formosum*** (Figure 28) to assess recovery from desiccation. In this endohydric moss, the relative water content (RWC) dropped to 40% before it reduced the net CO_2 uptake to zero. It took only 10-30% RWC upon rewetting for the CO_2 uptake to become positive after 9-18 days of desiccation. Net carbon balance returned after 0.3-1 hours. The F_v/F_m (= variable fluorescence / maximum fluorescence) recovery was inhibited in the light by protein-synthesis inhibitors, but had normal recovery in the dark. Without the inhibitors, the F_v/F_m reached ~80% of pre-desiccation levels within ~10 minutes of re-wetting, but it took 24 hours for full recovery.

Figure 28. ***Polytrichastrum formosum***, a moss that can drop to 40% relative water content before the net CO_2 uptake ceases. Photo by Des Callaghan, with permission.

Even aquatic bryophytes may not die following total desiccation. My experience with boiling ***Fontinalis*** (Figure 29) and with dead-looking mosses following snow-melt is that seemingly dead bryophytes may have living cells that initiate new growth. The desiccated tissues may not recover, but a few cells may be all that are needed to continue the population.

The seemingly drought-intolerant ***Fontinalis antipyretica*** (Figure 29) is actually drought tolerant, provided it is dried slowly (de Carvalho *et al*. 2011). This is consistent with its ability to survive late summer drought in the slow streams and vernal pools where it is common because the recession of water is slow and remaining water will permit the slow drying needed.

Figure 29. ***Fontinalis antipyretica*** in dry stream. This dead-looking moss will recover when water returns to the stream. Photo by Janice Glime.

Leakage and Membrane Repair

Dry mosses are essentially inactive. During this time, membranes often become distorted and leaky (Gupta 1977a. Viable tissues may become leaky due to the shock of sudden immersion, whereas injured or dead cells leak due to membrane disruption. Cruz de Carvalho *et al*. (2015) note that the rupture of membranes results in loss of electrolytes, and that this loss is greatest during rehydration following a rapid drying event. The ability to repair this damage may be an important factor that sets bryophytes apart from tracheophytes.

Upon rehydration, the less tolerant bryophytes initially spend time in repairing membrane damage caused by the dehydration. This is exemplified by the period of 4 to 24 hours that elapse prior to normal photosynthesis and respiration (Peterson & Mayo 1975; Dilks & Proctor 1976b; Proctor 1981). But before that repair occurs, leakage of both photosynthate and mineral ions can be severe, especially during the first two minutes following addition of water (Bewley 1974; Gupta 1977a. As in tracheophytes, the highly soluble K^+ is readily leaked during desiccation (Minibayeva & Beckett 2001; Table 2), but in the bryophytes, much of it is retained by cation exchange sites on the cell walls (Bates 1997). Fortunately, these retained ions can be re-absorbed by the cells during early rehydration. Material leaked into a culture medium is taken back into the cell within one hour (Bewley & Krochko 1982). Furthermore, at least in some liverworts, some of the lost photosynthate is resorbed (Noailles 1978).

In ***Syntrichia ruralis*** (Figure 21), slowly dried plants and undried controls lose only about half as much of electrolytes as do rapidly dried plants (Bewley & Krochko 1982). However, ***Cratoneuron filicinum*** (Figure 30) suffers more extensive loss under both slow and fast drying regimes and the loss is not reversible. Oliver and Bewley (1984b) interpreted these studies to mean that ***Syntrichia ruralis*** has membranes that undergo reversible changes during desiccation, but that these changes are incomplete when they are dried quickly. Upon rehydration it requires several minutes for the membranes to revert to their normal integrity. This mechanism to regain membrane integrity apparently is not working in the desiccation-intolerant ***Cratoneuron filicinum***.

Table 2. Loss of K^+ ions during rehydration following desiccation in bryophytes. **H** = hornwort; **LL** = leafy liverwort; **M** = moss; **TL** = thallose liverwort. Data from Minibayeva and Beckett (2001).

Anthoceros natalensis (H)	89%
Pellia epiphylla (TL)	83%
Hookeria lucens (M)	77%
Dumortiera hirsuta (TL)	55%
Atrichum androgynum (M)	45%
Sphagnum auriculatum (M)	38%
Plagiochila natalensis (LL)	21%
Rhodobryum roseum (M)	0%

Figure 30. ***Cratoneuron filicinum*** in hydrated state. Photo by Michael Lüth, with permission.

The leakage problem causes bryophytes to be vulnerable during frequent wetting/drying events. During each rehydration event, the plant must repair its cell membranes, and that requires energy. Frequent events with insufficient recovery time will eventually exhaust the resources within the cells. Because much repair is needed upon rehydration, it is critical that dry mosses retain the ability to synthesize ATP upon rewetting (Krochko *et al*. 1979). In ***Syntrichia ruralis*** (Figure 21), normal levels of ATP are regained in as little as 30 minutes. On the other hand, the hydrophytic ***Cratoneuron filicinum*** (Figure 30) slowly loses ATP after rewetting if the moss has been dried rapidly. Such behavior would prevent this moss from living in the desert, but poses no problem in its streamside habitat. However, Dhindsa (1985) suggested that it may be NADPH that is available immediately upon rehydration, produced by transhydrogenation from NADH during dark CO_2 fixation. Thus NADPH could be the important factor in repairing cellular damage by reductive biosynthesis of membrane components and other cellular constituents.

When the membrane first begins repair, there is a period of enhanced respiration during which the cell organelles regain normal appearance (Noailles 1978). Membrane repair occurs during this period of enhanced respiration, stopping the leakage (Farrar & Smith 1976; Richardson & Nieboer 1980). This is possible because, unlike the case in tracheophytes, protein synthesis begins immediately (Dhindsa & Bewley 1978), undoubtedly because of the conservation of **polyribosomes** (cluster of ribosomes connected with messenger RNA; play a role in peptide synthesis) in desiccation-tolerant bryophytes. Nothing is known about the role of action potentials in bryophytes and their possible role in membrane repair (Bates 2000), although Trebacz *et al.* (1994) have shown that Ca^{+2} influx and Cl^- efflux in the thallose liverwort ***Conocephalum conicum*** (Figure 24) result in depolarization of the cell membranes.

Mechanical damage is probably the primary cause of desiccation damage in cells. Membranes necessarily become contorted and folded during drying and cell shrinkage. In ***Syntrichia ruralis*** (Figure 21) pockets or **vesicles** (membranous spheres involved in transport or storage within cell) form on the **endoplasmic reticulum (**complex system of membranous stacks involved in membrane production in cell). Oliver and Bewley (1984b) suggested that these vesicles provide membrane material to be used for immediate repair upon rehydration. Other features that can help protect a cell from mechanical damage during dehydration include small cell size, small or no vacuoles, lack of **plasmodesmata** (tiny, membrane-line channels between adjacent cells), flexible cell walls, and reduced osmotic pressure (Iljin 1953, 1957). However, there is not a strong correlation of these attributes with desiccation-tolerant bryophytes. Bryophytes do have plasmodesmata, but electron microscopy is needed to discern them and few have been thus described; thus we cannot evaluate their correlation.

In support of Iljin's (1953, 1957) suggestion, some of the largest cells among bryophytes are those of the **Hookeriaceae**, a family of desiccation-sensitive mosses. And the **Pottiaceae** (including ***Syntrichia ruralis***) generally have small cells and live in dry places. But the vacuole correlation brings Iljin's suggested adaptations into question (Table 3), and even the cells of ***Syntrichia ruralis*** (Figure 21) shrink but are too rigid to collapse when they dry. One problem in attempting to determine just what happens as the cells dry is that in order to "fix" them for examination, we must partially rehydrate the cells (Oliver & Bewley 1984b). Until another method is forthcoming, we cannot observe what a dry cell looks like.

Table 3. Relative cell and vacuole sizes among bryophytes as listed by Oliver & Bewley (1984b).

	cell size	vacuoles
Desiccation tolerant		
Ceratodon purpureus	small	large
Syntrichia ruralis	small	small
Neckera crispa		small
Pleurozium schreberi	long & narrow	small
Barbula torquata	small	large
Triquetrella papillata	small	small
Desiccation sensitive		
Cratoneuron filicinum	long & narrow	small

Melick and Seppelt (1992, 1994) considered that the membrane integrity is restored rapidly and that intracellular carbohydrates likewise are replenished rapidly in the xerophytic ***Syntrichia caninervis*** (Figure 31)**.** In an interesting contrast to the membrane repair scenario, Singh *et al*. (1984) concluded that membranes of ***Syntrichia ruralis*** (Figure 21) remain intact during desiccation, at least down to 75% relative humidity (-400 bars). The cellular membranes retain their phospholipid bilayers, and during dehydration the cytoplasmic vesicles form layers of membranes under the **plasmalemma** (cell membrane), appearing to fuse with the surface membrane. They

concluded that the cellular membranes are conserved and ready to expand upon rehydration. Wu *et al*. (2013) found a similar conservation of cell membranes in the desert moss ***Syntrichia caninervis***.

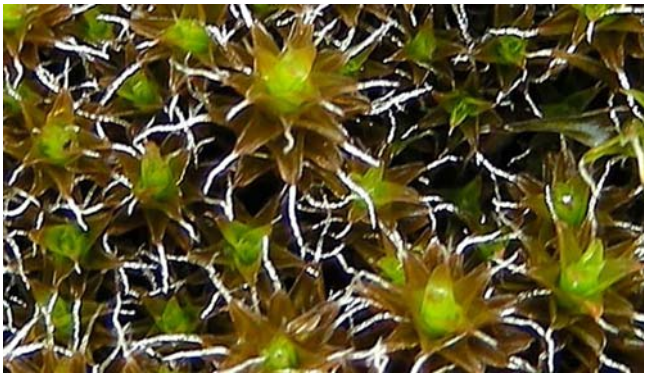

Figure 31. ***Syntrichia caninervis***, a desiccation-tolerant desert moss. Photo by Michael Lüth, with permission.

Based on these various responses of the cell membranes, it is not surprising that Oliver *et al*. (1993) found that electrolyte leakage alone was not a reliable measure of desiccation tolerance in ***Syntrichia ruralis*** (Figure 21). Instead, Stewart and Lee (1972) reported that NADP-linked glyceraldehyde phosphate dehydrogenase is affected by desiccation, and Bewley and his coworkers (Bewley 1972, 1973a, b, 1974, 1979, Bewley & Gwozdz 1975) have carefully documented the loss of polyribosomes and their effect on the ability of the cells to synthesize proteins. Oliver *et al*. (1993) found that comparison of ability to synthesize protein in hydrated and desiccated-rehydrated mosses was the best measure of the capabilities of three ***Syntrichia*** species to repair damage and thus to exhibit tolerance to desiccation.

Pulse release occurs in ***Hylocomium splendens*** (Figure 32) during rehydration, returning carbon and other nutrients, especially potassium, to the soil (Wilson & Coxson 1999). These mosses are able to concentrate carbon and nutrients from atmospheric sources and return them in concentrated form during these pulse releases caused by rainfall striking damaged membranes.

Figure 32. ***Hylocomium splendens*** on forest floor, a species that grows as well with 6 or 7 days of hydration a week, but not with other hydration regimens. Photo by Amadej Trnkoczy, through Creative Commons.

Protein Degradation and Ubiquitin

O'Mahony and Oliver (1999) compared the role of **ubiquitin** in the grass *Sporobolus stapfianus* and the desiccation-tolerant moss ***Syntrichia ruralis*** (Figure 21Figure 31) as a mediator of protein degradation. They found that in *S. stapfianus* the ubiquitin exhibited greater accumulation during drying and rehydration, but that it was hardly detectable in the desiccated tissue. A depletion of ubiquitin monomer levels indicates an increase in protein degradation. In ***Syntrichia ruralis***, the ubiquitin transcripts were stable in the dried tissue. The moss contrasted to the grass in that conjugated ubiquitin, indicative of proteins targeted for removal, was detectable in the moss only during slow drying, whereas it was present in all samples of the grass. O'Mahony and Oliver concluded that ***S. ruralis*** has stable ubiquitin transcripts that rapidly translate during rehydration to permit rapid initiation of cellular repair by degrading targeted proteins, whereas *Sporobolus stapfianus* requires several hours to replace its depleted ubiquitin supply.

Respiration

Respiration during recovery can vary considerably among species. Gupta (1977b) found that after 48 hours of desiccation at 0 and 50% relative humidity, rewetting for 32 hours varied in O_2 uptake from 2X in ***Mnium hornum*** (Figure 33) and ***Porella platyphylla*** (Figure 34) to 6X in ***Scapania undulata*** (Figure 35). This may in part be due to the presence of many respiring microorganisms that benefit from the leaked cellular contents (Gupta 1977a, b). Methods for measuring recovery processes need to take this microorganism respiration into account.

Figure 33. ***Mnium hornum***, a species that doubles its oxygen uptake upon rehydration. Photo by Michael Lüth, with permission.

Reactive Oxygen Species

The greatest damage to cells is caused by reactive oxygen species (Kranner *et al*. 2002; Beckett *et al*. 2004). Among the bryophytes, Beckett *et al*. (2004) demonstrated this in desiccated thalli of the liverwort ***Dumortiera hirsuta*** (Figure 36). In fact, this species produces extracellular superoxide at high rates under normal conditions, but that following mild desiccation stress, it produces considerably

more during rehydration. They postulated that it might have a role in defense against pathogens.

Figure 34. ***Porella platyphylla***, a species that doubles its oxygen uptake upon rehydration. Photo by Janice Glime.

Figure 35. ***Scapania undulata***, a species that has 6X as much oxygen uptake when recovering from desiccation. Photo by David Holyoak, with permission.

Figure 36. ***Dumortiera hirsuta***, a species that produces extracellular superoxide at a high rate, increasing production following mild desiccation stress. Photo by Paul Davison, with permission,

Even aquatic mosses like ***Fontinalis antipyretica*** (Figure 29) has protection from reactive oxygen species. de Carvalho *et al*. (2012) found that when this species was dried slowly and rehydrated, it had a lower production of reactive oxygen species (ROS). This reduced the cellular damage. As it rehydrated, it had an initial high oxygen consumption burst; de Carvalho and coworkers suggested that this may have been due to the burst of ROS production.

Photosynthesis

The desert moss ***Syntrichia caninervis*** (Figure 31) is a dominant soil crust bryophyte in deserts. As such, it has often served as a model for desiccation tolerance. Its photosynthesis recovers quickly following a dehydration-rehydration cycle (Li *et al*. 2010). The recovery occurs in two phases. The initial phase occurs in only three minutes, with a quick increase in maximal quantum efficiency of **PS II** (F_v/F_m) (photosystem II variable vs maximum fluorescence). In only 0.5 minutes from the onset of rehydration, over 50% of the PS II activities resume, including excitation energy transfer, oxygen evolution, charge separation, and electron transport. The second phase is slower and is dominated by an increase of **plastoquinone** (PQ; molecule involved in the electron transport chain in the light-dependent reactions of photosynthesis) reduction and accomplishing equilibrium of the energy transport from the inner chlorophyll antenna system to the reaction center of PS II. No *de novo* chloroplast protein synthesis is needed for this initial recovery of the PS II photochemical activity. The rapid recovery depends on chlorophyll synthesis, quick structural reorganization of PS II, and fast restoration of PS II activity without chloroplast protein synthesis.

Zhang *et al*. (2011) found that in ***Syntrichia caninervis*** (Figure 31), an ectohydric desert moss, minimum and maximum fluorescence and photosynthetic yield recovered quickly when the shoots were rehydrated in the dark. In fact, this species reached 90% of its 30-minute yield rate within the first minute, a phenomenon that was possible because of the lack of damage to membranes.

In ***Syntrichia caninervis*** (Figure 31) remoistening elicited rapid recovery of both fluorescence and photosynthetic yield (F_v/F_m) in the dark, reaching within 1 minute 90% of the value attained in 30 minutes (Zhang *et al*. 2011). The optimum moisture level falls in a narrow range, with chlorophyll fluorescence decreasing both above and below that moisture range. In its desert habitat, it is able to use dew, fog, rain, and melting snow as sources of moisture to permit photosynthesis.

At least in some species, rehydration results in an initial period of rapid respiration (Dilks & Proctor 1976b). In several temperate/boreal bryophytes, this rapid period of respiration is followed by a progressive recovery of photosynthesis generally lasting 1-6 hours. ***Anomodon viticulosus*** (Figure 37), a xerophytic species of well-drained, lightly shaded, base-rich or calcareous rocks and dry stone walls, reached its **compensation point** (photosynthesis = respiration) within a few minutes of hydration, whereas it required about 4 hours for ***Rhytidiadelphus loreus*** (Figure 38), a mesophytic forest floor species. For desiccation-tolerant bryophytes such as ***Anomodon viticulosus***, ***Racomitrium lanuginosum***

(Figure 39), and ***Rhytidiadelphus loreus***, recovery of photosynthesis upon rehydration is rapid (Proctor & Smirnoff 2000). This rapid recovery necessarily requires pre-existing proteins; *de novo* protein synthesis is generally very limited (Proctor 2001).

Dhindsa (1985) determined that desiccation-tolerant mosses such as ***Syntrichia ruralis*** (Figure 21) remain active and fix CO_2 (dark fixation) at an undiminished rate until tissue losses are about 60% of the initial fresh mass, whereas in the intolerant ***Cratoneuron filicinum*** (Figure 30) dark fixation of CO_2 slowly declines as the moss dehydrates. After that, water stress occurs, the moss rapidly proceeds to suspended metabolism, and CO_2 fixation rapidly ceases. Following rehydration, ***S. ruralis*** immediately begins CO_2 fixation, but ***C. filicinum*** does not. For tracheophytes, this recovery system has been perfected primarily in seeds that return from their suspended metabolism by metabolizing starches to sugars for the rapid supply of energy needed to grow and attain photosynthesis. Even in the desert ephemerals, the return process is slow and the frequency of wetting and drying suffered and survived by some desert bryophytes is unattainable by any tracheophyte (Proctor 2000b, 2001).

Figure 37. ***Anomodon viticulosus***, a moss that rapidly rehydrates and is ready for photosynthesis. Photo by Michael Lüth, with permission.

Figure 38. ***Rhytidiadelphus loreus*** on the forest floor, a species that is rapid to regain photosynthetic activity after rehydration, but slower than ***Anomodon viticulosus***. Photo by Michael Lüth, with permission.

Figure 39. ***Racomitrium lanuginosum*** on rock, a species that rapidly regains photosynthetic activity after rehydration. Photo by Michael Lüth, with permission.

Guschina *et al*. (2002) related the rapid recovery to the stress hormone **ABA** in the mesophytic moss ***Atrichum androgynum*** (Figure 40). Changes in phosphoglyceride composition due to water stress indicate an activation of phospholipase D and of phosphatidylinositol metabolism. During rehydration, phosphoglyceride composition recovers close to the original levels. Thylakoid lipids and chlorophyll decline during dehydration, accounting for the loss of photosynthesis. Treatment with ABA reduces the overall extent of changes, probably by reducing lipid changes, thus protecting against membrane damage. But can the moss produce its own ABA? And is it inducible?

Figure 40. ***Atrichum androgynum***, a moss that uses ABA to aid in rapid recovery from desiccation. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Architectural Changes

We know that many bryophytes, including ***Syntrichia ruralis*** (Figure 21), undergo multiple architectural changes as they dry (Hamerlynck *et al*. 2000). This results in changes to the surface reflectance. Hamerlynck *et al*. found a sigmoidal (logistic) relationship between the relative humidity and the deviation of the moss mat temperature from its dew point, indicating a slow, then rapid, then slow change in the temperature of the mat, and a concomitant change in its water loss. The conditions of drying affect the ability of this species to use thermal

dissipation of excess light energy, thus affecting potential damage to the chlorophyll.

Breuil-Sée (1994) examined the cell interior upon rehydration of the thallose liverwort ***Riccia macrocarpa*** (Figure 41) after 25 years of dehydration in a herbarium. Whereas most bryophytes revive to normal metabolism in a few hours, this 25-year-dry bryophyte required nine days. Cytological evidence of its revival included enlargement of **nucleoli** (sites of ribosome synthesis and assembly in nucleus), evidence for protein synthesis. The dehydrated liverworts had few **mitochondria** (site in cell that generates most of the ATP) and the chloroplasts lacked starch. Its preparation for desiccation was evidenced in granular cytoplasm with many **osmiophilic globules** (lipid-containing bodies in chloroplast), especially along the cell wall. Features already known for dry spores and seeds, such as presence of **plasmodesmata** (microscopic channels which traverse cell walls of plant cells, enabling transport and communication between cells), but absence of **dictyosomes** [stacks of flat, membrane-bound cavities (cisternae) where proteins are stored and that comprise the Golgi apparatus] and **endoplasmic reticulum** (**ER**; interconnected network of flattened, membrane-enclosed sacs or tubes known as cisternae; inner core of cytoplasm and membranes of ER are continuous with outer membrane of nuclear envelope), were evident. The transition of ***R. macrocarpa*** toward active metabolism upon rewetting was marked by 1) enlargement of nucleolus; 2) important modification of nucleus; 3) amplification of endoplasmic reticulum, Golgi, chloroplasts, mitochondria, and vacuoles; 4) disappearance of lipid reserves; 5) synthesis of starch in chloroplasts; 6) cytoplasm densification.

Figure 41. ***Riccia macrocarpa***, a species that resumed normal metabolism upon rehydration after 25 years in a dry state. Photo by Michael Lüth, with permission.

The protonemata are important survival structures in some habitats and for some species. Pressel and Duckett (2010) found that in their experiments the protonemata could survive slow, but not fast drying. During dehydration, the cell experiences vacuolar fragmentation, reorganization of the endomembranes, changes in cell wall thickness, changes in the morphology of plastids and mitochondria, and a controlled dismantling of the cytoskeleton. These events cannot occur during fast drying. Externally applied abscisic acid mimicked the effects of slow drying, permitting the protonemata to survive.

Cellular Changes

Oliver *et al*. (2005) indicated that desiccated cells appear to be intact. Cellular disruption occurs upon rehydration as water is taken up rapidly. Nevertheless, the cellular integrity returns rapidly.

Desert mosses can have remarkable durability to desiccation. Moore *et al*. (1982) found that ***Didymodon torquatus*** (Figure 42) can survive 18 months of desiccation at a water content of only 5% or less. Nevertheless, after only 24 weeks of desiccation, the photosynthetic and respiratory rate upon rehydration were less than that of fresh (hydrated) materials. What is interesting is that in shorter time periods this species returned to control levels within one hour of rewetting. ***Triquetrella papillata*** (Figure 43), however, had a shorter survival time. In both species, the integrity of the organelles was maintained during short periods of desiccation, but that integrity diminished progressively with time. Net photosynthesis was delayed, apparently due to the disappearance of chloroplast and mitochondrial membranes and loss of internal structure.

Figure 42. ***Didymodon torquatus*** dry, a species that can survive extreme desiccation for 18 months. Photo from Canberra Nature Map, through Creative Commons.

Figure 43. ***Triquetrella papillata*** dry, a species that survives a short period of drought. Photo by David Tng, with permission.

Despite this degradation with time, Breuil-Sée (1994) found that the thallose liverwort ***Riccia macrocarpa*** revived after 23 years of drying. Upon rehydration, the endoplasmic reticulum became extended and the nucleolar volume increased, but these events were not observed until day 9.

Leptoid Recovery

Pressel (2006) pointed out the lack of study on the behavior of leptoid cells following rehydration. Using the endohydric moss ***Polytrichastrum formosum***, she documented that desiccation cause dramatic changes in leptoid tissues. The endoplasmic microtubules disappear; the nucleus, mitochondria, and plastids become rounded and longitudinal alignment of the organelles disappears. Cytoplasmic polarity is at least partly retained. Instead of the prominent stacks of endoplasmic reticulum that characterize the hydrated state, the membranous tubules are arranged at right angles to the main cellular axis. The cytoplasm of the leptoids is filled with small vacuoles. The plasmalemma deposits ingrowths of cell wall material, forming labyrinthine extensions. The plasmodesmata of apical meristematic and stem parenchyma cells seem unaffected by dehydration, but in the leptoids they become plugged with electron-opaque material. Starch is depleted in the parenchyma cells adjoining the leptoids. In control plants, the cellular structure is completely re-established in 12-24 hours, but this is not the case in cells treated with oryzalin, a microtubule-disrupting drug. Pressel concluded that the microtubular cytoskeleton is key in the rapid re-establishment of the cytoplasmic architecture of leptoids during rehydration.

Chloroplast Recovery

Proctor *et al*. (2007) found that thylakoids, grana, and mitochondrial cristae of ***Polytrichastrum formosum*** (Figure 28) remain intact during drying and re-wetting. Nevertheless, the form of organelles changes quite noticeably. Chloroplasts lose their prominent lobes, becoming rounded when desiccated. They require ~24 hours to return to their normal shape. Photosynthesis likewise requires 24 hours for full recovery, but is independent of protein synthesis. It appears that the physical structure of the chloroplast remains the same, but that the spatial relationships among the components is altered during dehydration. Proctor *et al*. concluded that the cytoskeleton has a significant role in the bryophyte desiccation response.

Wood and coworkers may have a partial answer to the recovery of the chloroplasts following desiccation (Wood & Oliver 1999; Wood *et al*. 1999; Zeng & Wood 2000; Zeng *et al.* 2002). There is a change in gene expression during rehydration of ***Syntrichia ruralis*** (Figure 21), suggesting that new proteins are being made. It appears that some of these proteins may account for the rapid chlorophyll recovery. We now understand that the moss prepares for its desiccation and rehydration events by altering gene expression in response to desiccation, then altering translational controls as it rehydrates. When the drying rate has been slow, **mRNPs** (messenger ribonucleoprotein particles) are formed in the drying plants, and within these particles they sequester **rehydrin** mRNA (mRNA transcripts used during rehydration). It appears that one of these rehydrins may be responsible for the production of antioxidants during rehydration (Oliver *et al*. 1997). It is the production of these mRNPs that makes slow dehydration so important to the recovery (Oliver 1996). If the moss is dried rapidly, it must make these when it rehydrates.

Wood and coworkers (1999) supported this discovery that ***Syntrichia ruralis*** (Figure 21) has an active recovery mechanism that is induced by rehydration. It makes a set of polypeptides that are not present at any time except during rehydration. These polypeptides were products of a large number of as yet unidentified plant genes and 71% of these are unknown in other plant phyla.

Among these are most likely the cDNA *Rp115* identified by Zeng and Wood in 2000 and which is conserved as mRNA in desiccated gametophytes, and two additional cDNA units (***Elipa & Elipb***), both of which have significant similarity to Early Light-Inducible Proteins (ELIP; Zeng *et al.* 2002). The **ELIP** group (coded by *Elip* genes) includes over 100 stress-inducible proteins (Heddad & Adamska 2002). They are produced in response to light stress and accumulate in photosynthetic membranes where they have a photoprotective function. They are closely related to the light-harvesting chlorophyll *a*/*b*-binding antenna proteins of photosystems I and II. Because of the response of *Elipa* genes to slow desiccation, rapid desiccation/rehydration, salinity, ABA, and rehydration in high light, and the response of *Elipb* genes to ABA or rehydration in high light, Zeng *et al*. (2002) suggested that ELIPa and ELIPb provide an adaptive response to the photodamage that is likely to occur within a moss chloroplast during desiccation, most likely playing an important role in protecting and/or repairing the photosynthetic apparatus.

In support of this hypothesis, Hutin and coworkers (2003) found that when they suppressed this rapid accumulation of ELIPs during high-light stress in a mutant of the flowering plant *Arabidopsis thaliana*, the leaves became bleached and cells suffered extensive photooxidative damage, but when the plant was permitted to accumulate ELIPs before the stress, they exhibited normal phototolerance. Hence, it appears that they do indeed perform a photoprotective function, either by binding the chlorophylls that are released during turnover of the pigment-binding proteins or by stabilizing the proper assembly of those proteins when they are being subjected to high-light stress.

Lüttge *et al*. (2008) found that the three poikilohydric species ***Campylopus savannarum***, ***Rhacocarpus fontinaloides***, and ***Ptychomitrium vaginatum*** achieved photo-oxidative protection in their light-adapted state. This was accomplished by a reduction of chlorophyll fluorescence to near zero. When rewet, they have a very fast recovery in the first 5 minutes, but require more than 80 minutes to reach an equilibrium. Even though they occupy different niches on their rock outcrop habitat, they had similar recovery kinetics, with only their photosynthetic capacity differing slightly.

Photodamage

For the most desiccation-tolerant mosses, those from **xeric** (dry) habitats, **fluorescence** (emission of light of longer wavelength due to absorbance of light from outside source) levels upon rehydration indicate that the

photosynthetic apparatus is fully functional, unlike that of mosses from **hydric** (wet) and **mesic** (moderate) habitats (Deltoro *et al*. 1998a; Marschall & Proctor 1999). **Photoinhibition** (inhibition of photosynthesis by light) is a well-known consequence of desiccation because the **light quenching** is greatly diminished or absent. Only the desiccation-tolerant bryophytes exhibited photo-quenching at low water content in these experiments. Deltoro and coworkers (1998a, b) suggest that this loss of photosynthetic capability in **mesophytic** bryophytes might be not only a consequence of photoinhibition, but also a result of membrane damage, as indicated by the large K^+ leakage. In desiccation-tolerant taxa, they suggest, the ability to enhance the dissipation of thermal energy during dehydration might permit them to take advantage of the erratic water supply in places like the desert and decrease the problems of photodamage during the dehydration stage, thus permitting them to recover quickly.

Measuring Damage

Records of survivability may sometimes be misleading. For example, Makinde and Fajuke (2009) reported survival based on microscopic views of vacuoles as soon as the cells were hydrated without any verification by regeneration, a true test for survival.

Not only do different species respond differently, but leaves and cells vary on the same plant. Streusand and Ikuma (1986) suggested a protocol that requires a large number of cells counted in a given leaf, a large number of leaves, and a large number of shoots. They considered 10 cells in 6 areas of each of 6 leaves per shoot on 10 shoots to be adequate and it provided a near perfect correlation with shoot survival in experiments with different desiccation protocols.

Factors Affecting Recovery

Temperature

In the dry state, plants are much more resilient at temperature extremes than are hydrated plants. As Alpert (2000) pointed out, some can survive as low as -272°C or as high as 100°C. He raises two questions regarding survival of desiccation: What are the mechanisms by which plants tolerate desiccation? and Why are desiccation-tolerant plants not more ecologically widespread? In general, they seem to require protection from oxidants and from loss of configuration of the macromolecules during their dehydration period.

Drying Speed

Many studies have indicated that drying speed is important to successful recovery from desiccation (Krochko *et al*. 1978; Schonbeck & Bewley 1981a; Greenwood & Stark 2014). This varies, based on **inducible** vs **constitutive** desiccation tolerance responses. Those that are harmed by rapid drying, but that recover after slow drying, are able to use an **inducible** system (one that develops in response to desiccation) to protect them against desiccation effects. The slower timing is required for that inducible system to prepare. This system is more likely to be effective in aquatic or wet-habitat species, as demonstrated by the semi-aquatic ***Cratoneuron filicinum*** (Figure 30). In this species, rapid drying results in considerable disruption of the cell contents, whereas following slow drying some cells are able to maintain their cellular organization and integrity. Protein synthesis is reduced upon rehydration under both very slow and rapid drying, but these effects are reversible down to a water loss of 50% of fresh weight. Unlike the observations of Dilks and Proctor (1976b) on several terrestrial boreal/temperate bryophytes, respiration does not occur when the moss is rewet after rapid drying.

Even in such xerophytic taxa as ***Syntrichia ruralis*** (Figure 21), rapid drying causes visible injury, reduced total chlorophyll, reduction in chlorophyll *a:b* ratio, greatly enhanced electrolyte loss, and consequent inhibition of gross photosynthesis (Schonbeck & Bewley 1981a). Partial desiccation for 1-3 hours before rapid drying will eliminate this injury, suggesting that the moss requires time to prepare for its recovery. When ***Syntrichia ruralis*** and hydrophytic ***Cratoneuron filicinum*** (Figure 30) are dried rapidly, the chloroplasts and mitochondria swell and lose their integrity upon rewetting (Krochko *et al*. 1978, 1979), but ***S. ruralis*** regains normal appearance within 24 hours, whereas ***C. filicinum*** loses its cell contents and shows considerable cell degradation. However, if the cells are dried more slowly (*e.g.* 12 hours at 75% RH), both species recover within 24 hours. Dhindsa and Bewley (1978) attribute the ability of ***Syntrichia ruralis*** to survive this swelling of organelles to their ability to synthesize or retain sufficiently the enzymes needed for repair.

Hamerlynck *et al*. (2002) later found that ***Syntrichia ruralis*** (Figure 21) grown in high light intensity has greater desiccation tolerance than plants grown in the shade, but that those plants growing in the shade may benefit from their longer periods of metabolic activity and greater acquisition of resources, permitting them to adjust sufficiently to canopy openings and other disturbances.

Proctor (2003) subjected both desiccation-tolerant and moderately desiccation-tolerant species to drying for various periods up to 240 days. The more desiccation tolerant species (***Grimmia pulvinata***, ***Syntrichia ruralis***, ***Andreaea rothii***, ***Racomitrium lanuginosum***, ***R. aquaticum***, ***Leucodon sciuroides***, ***Pleurochaete squarrosa***, ***Ulota crispa***) had their best long-term survival (>30-120 days) at ~-100 to -200 MPa (20-45% r.h.). The moderately desiccation-tolerant ***Anomodon viticulosus***, ***Porella platyphylla***, and ***P. obtusata*** survived best at the highest humidity used, -41 MPa (74% r.h.). The lower humidities would speed desiccation and only the most tolerant could survive.

Greenwood and Stark (2014) determined that when **Fv/Fm** are less than 0.1, ***Physcomitrella patens*** fails to regenerate. The Fv/Fm fluorescence is the standard measurement for stress in plants, testing whether or not plant stress affects photosystem II in a dark adapted state. Fv refers to fluorescence in its variable state; Fm is maximum fluorescence. They used a process of drying that permitted as long as 284 hours for drying and found a significant increase over results obtained using salt solutions to create desired moisture conditions. Survival rates and chlorophyll fluorescence both improved and tissue regeneration time was shortened, demonstrating a much greater desiccation tolerance than was previously known for this species.

Frequency of Dehydration/Rehydration

Upon rehydration, it requires time to repair membranes and regain the energy lost. Oliver and Bewley (1984a) have demonstrated that in some mosses the first 24 hours are spent in repair, and it is only after that period that there is a net photosynthetic gain. For this reason, frequent short sequences of desiccation can be devastating to many species, whereas the same moss can endure long periods of desiccation. For example, ***Didymodon vinealis*** (Figure 44) (Moore *et al*. 1982) recovered completely within one hour of rewetting after 18 months of desiccation at less than 5% relative water content. However, following short periods of desiccation, the integrity of the organelles was progressively lost, including membrane loss from chloroplasts and mitochondria. Repairing this damage resulted in delays in net photosynthetic gain.

Figure 44. ***Didymodon vinealis***, a moss that is able to recover within one hour of hydration after 18 months of desiccation. Photo by Jan-Peter Frahm, with permission.

Dilks and Proctor (1976b) likewise promoted the understanding that frequency of desiccation can be more important than duration. Using 6 days wet – 1 day dry conditions compared to 1 day wet – 6 days dry, 1 day wet – 1 day dry, and 7 days wet – 7 days dry for a period of 18 weeks, they showed that ***Hylocomium splendens*** (Figure 32) grew equally well in continuous moist conditions and in 6 days wet – 1 day dry (32% relative humidity). However, there was little or no growth among the other treatments. In ***Rhytidiadelphus loreus*** (Figure 45), growth was best in continuously hydrated mosses, then 6 wet – 1 dry day mosses, then 7 wet – 7dry day mosses. There was essentially no growth in the other treatments. Responses by ***Syntrichia ruralis*** (syn.=*Tortula ruraliformis*; Figure 21) were so variable that they could not be interpreted. However, Dilks and Proctor were able to conclude that 63 wet-dry cycles were not harmful, but that constant moist conditions were harmful in this highly desiccation-tolerant moss. ***Rhytidiadelphus loreus***, unlike the other mosses, showed a **hardening** effect (process of increasing resistance to stress factor), indicating less effect from drought as more droughts occurred. ***Syntrichia ruralis*** is always drought-ready so hardening is not discernible.

To test the impact of intermittent desiccation on reproductive success of xerophytic mosses, Mishler and Newton (1988) measured the success of germination of both fragments and spores of four ***Syntrichia*** species [***S. ruralis*** (Figure 21), ***S. princeps*** (Figure 46), ***S. norvegica*** (Figure 47), ***S. laevipila*** (Figure 48)] in continuous versus intermittent moisture. Only ***S. princeps*** fragments did slightly better under the intermittent moisture conditions, as did its spore germination. In all other species, the continuous hydration seemed beneficial to the spores. Establishment success was quite different. None of the spore-derived protonemata gave rise to stems (Mishler & Newton 1988). Fragments, however, produced numerous stems both from protonemata and directly from the fragments, independent of the hydration conditions. Most likely some other physiological or environmental cue was missing for the spore-derived protonemata.

Figure 45. ***Rhytidiadelphus loreus***, a moss that undergoes drought hardening. Photo by Michael Lüth, with permission.

Figure 46. ***Syntrichia princeps***, a moss that has better germination of spores and fragments under intermittent moisture than under continuous moisture. Photo by Jan-Peter Frahm, with permission.

Figure 47. ***Syntrichia norvegica***, a species in which fragments and spores germinate better in continuous moisture than in other moisture regimes. Photo by Michael Lüth, with permission.

Figure 48. ***Syntrichia laevipila***, a species in which fragments and spores germinate better in continuous moisture than in discontinuous regimes. Photo by Jonathan Sleath, with permission.

In other species, high resistance is attained after several short exposures to drought (Clausen 1952; Abel 1956; Patterson 1964; Dilks & Proctor 1976a, b). We know that ***Syntrichia ruralis*** (Figure 21) is capable of drought hardening (Schonbeck & Bewley 1981b). When subjected to daily episodes of desiccation and rehydration, it develops a greater desiccation tolerance. However, the wet-dry cycle may be of less importance for boreal forest mosses. Hanslin and coworkers (2001) exposed ***Dicranum majus*** (Figure 49) and ***Rhytidiadelphus loreus*** (Figure 38) to various watering regimes and found that responses, while differing greatly, lacked any consistent pattern. However, the relative growth rate increased with the length of the wet-dry cycle, provided the total number of wet and dry days remained equal, suggesting that these taxa probably would be unable to take advantage of night-time dew accompanied by day-time drought, but they are adapted to the more weekly or monthly wet-dry cycles typical of the boreal forest.

Davey (1997) showed that Antarctic hydric mosses are susceptible to damage by frequent wetting and drying, but that was not the case for the mesic and xeric mosses, which seemingly were adapted to frequent wet/dry cycles. All the mosses suffered a greater loss of photosynthetic rate as the duration of the dehydration periods increased. Davey suggested that mosses from the drier habitats were adapted to use short periods of rehydration. This is consistent with the use of late night/early morning moisture from clouds in xeric African montane sites and other habitats where nighttime dew is the major source of water. Csintalan and coworkers (2000) supported this concept with their work on ***Syntrichia ruralis*** (Figure 21) in dry grasslands. They found that the moss absorbed progressive amounts of water through the night, permitting it to obtain about 1.5 hours of net photosynthetic gain immediately after dawn. Although this gain on many days may not be enough to offset the carbon loss during the remainder of the day, it does contribute to the overall carbon gain and may permit the moss to gain on a yearly scale when added to those occasions when more dew or moisture is available.

Figure 49. ***Dicranum majus***, a moss that seems to do best when the number of wet and dry days are about equal. Photo by Michael Lüth, with permission.

Carbon Balance

The bottom line in the dehydration/rehydration cycle over the course of the lifetime of the bryophyte is carbon gain (Alpert 2000). Short-term rehydration events can use more carbon in repair processes than can be gained from photosynthesis once everything is working properly. For those species that can regain photosynthetic activity within the first minute, an array of water sources becomes available, including dew and fog in addition to rain and snow. These may be the same species that experience rapid drying because of a desert-like habitat. For these, constitutive desiccation tolerance is important. This strategy may include structural adaptations that slow drying and cellular mechanisms that preserve the integrity of the cellular organelles. But as demonstrated in the desert moss ***Pterygoneurum lamellatum*** (Figure 50), tolerance to slow drying can be inducible (Stark *et al*. 2013).

Oliver *et al*. (1993) proposed a three-part strategy of tolerance that is based on carbon balance, damage limitation, and cellular repair. To support this they used protein synthesis following desiccation/rehydration in three desiccation-tolerant moss species: ***Syntrichia caninervis*** (Figure 31), ***S. ruralis*** (Figure 21), and ***S. norvegica*** (Figure 47). Using this as a measure of repair, they ranked the tolerance of these species as ***S. caninervis*** > ***S. ruralis*** > ***S. norvegic***a.

Figure 50. ***Pterygoneurum lamellatum***, a desert moss with inducible desiccation tolerance when dried slowly. Photo by Michael Lüth, with permission.

Implications

It appears that characteristics suggested for tracheophytes to permit them to survive desiccation (Iljin 1953, 1957) do not apply well to bryophytes. Rather, Oliver and Bewley (1984b) suggested that tolerant species must do three things to survive drying: (1) limit damage to a level that can be repaired; (2) maintain physiological integrity of the cell so metabolism can quickly reactivate during rehydration; (3) put repair mechanisms into effect upon rehydration, especially to regain integrity of membranes.

Many questions remain to be answered in understanding the recovery process in bryophytes. When studying the grass *Sporobolus stapfianus*, Neale *et al*. (2000) found that *Elip* genes were expressed differently in tissues that were desiccation tolerant than in those that were desiccation sensitive and suggested that there are unique gene regulatory processes occurring as desiccation ensues, permitting different drought-responsive genes to be expressed at different stages during water loss. Since these genes have been identified in bryophytes, it is likely that Zeng *et al*. (2002) are correct in their suggestion of a photoprotective role during the dehydration state of bryophytes.

As summarized by Oliver *et al*. (2005), desiccation tolerance is a primitive trait, a necessary trait for invasion of land. In bryophytes, two aspects permit their survival: constitutive cellular protection and effective recovery/repair mechanism. (To this we must add inducible tolerance in at least some bryophytes.) But upon recovery, the cells behave like any container of light-weight objects that suddenly gets an influx of water, being disrupted initially. Nevertheless, the cell soon regains its integrity. Photosynthetic activity seems little affected and recovers quickly. LEA proteins proliferate, but their role is unknown, perhaps functioning to restructure the membranes and stabilize the cell. More questions!

Summary

Desiccation tolerance most likely originated in the early land bryophytes in their colonization of land. Yet, they remain almost unique in their ability to tolerate desiccation in the vegetative state. Bryophyte gametophytes recover from desiccation by the actions of numerous **rehydration proteins**, including **rehydrins**, and **rapid membrane repair**. The rapidity is dependent upon slow dehydration that gives the bryophyte time to make mRNPs and is provided by a rehydration-inducible recovery mechanism in which new proteins are synthesized rapidly (Oliver 1996). The rapid recovery is complemented by enlargement of the nucleolus, amplification of the endoplasmic reticulum, Golgi, chloroplasts, mitochondria, and vacuoles, disappearance of lipid reserves, and synthesis of starch in chloroplasts during rewetting.

Photosynthesis resumes almost immediately, reaching normal levels within 24 hours, indicating the readiness of the chloroplasts. Because of the resources needed for recovery, short periods of rehydration between frequent drying periods deplete resources and are more harmful than long dry periods, issuing foreboding for moss gardeners.

Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself.

Literature Cited

Abel, W. O. 1956. Die Austrocknungsresistenz der Laubmoose. Anz. Osterr. Akad. Wiss. Math. Naturwiss. KI. 165: 619-707. In: During, H. J. 1979. Life Strategies of Bryophytes: a preliminary review. Lindbergia 5: 2-18.

Alpert, P. 2000. The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol. 151: 5-17.

Alpert, P. and Oechel, W. C. 1985. Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. Ecology 66: 660-669.

Alpert, P. and Oechel, W. C. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. Amer. J. Bot. 74: 1787-1796.

Bates, J. W. 1997. Effects of intermittent desiccation on nutrient economy and growth of two ecologically contrasted mosses. Ann. Bot. 79: 299-309.

Bates, J. W. 2000. Mineral nutrition, substratum ecology, and pollution. In: Shaw, A. J. and Goffinet, B. (eds.). Bryophyte Biology, Cambridge University Press, Cambridge, UK, pp. 248-311.

Beckett, R. P., Minibayeva, F. V., Lüthje, S., and Böttger, M. 2004. Reactive oxygen species metabolism in desiccation-stressed thalli of the liverwort ***Dumortiera hirsuta***. Physiol. Plant. 122: 3-10.

Bewley, J. D. 1972. The conservation of polyribosomes in the moss *Tortula ruralis* during total desiccation. J. Exper. Bot. 23: 692-698.

Bewley, J. D. 1973a. Desiccation and protein synthesis in *Tortula ruralis*. Can. J. Bot. 51: 203-206.

Bewley, J. D. 1973b. The effects of liquid nitrogen temperatures on protein and RNA synthesis in the moss *Tortula ruralis*. Plant Sci. Letters 1: 303-308.

Bewley, J. D. 1974. Protein synthesis and polyribosome stability upon desiccation of the aquatic moss *Hygrohypnum luridum*. Can. J. Bot. 52: 423-427.

Bewley, J. D. 1979. Physiological aspects of desiccation tolerance. Ann. Rev. Plant Physiol. 30: 195-238.

Bewley, J. D. and Gwozdz, E. A. 1975. Plant desiccation and protein synthesis II. On the relationship between endogenous adenosine triphosphate levels and protein-synthesizing capacity. Plant Physiol. 55: 1110-1114.

Bewley, J. D. and Krochko, J. E. 1982. Desiccation-tolerance. In: Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H. (eds.). Physiological Plant Ecology. II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology, New Series, vol. 12 B, Springer-Verlag, Berlin, Heidelberg, pp. 325-378.

Breuil-Sée, A. 1993. Bryological notes - recorded desiccation-survival times in bryophytes. J. Bryol. 17: 679-684.

Breuil-Sée, A. 1994. Reviviscence d' un bryophyte en anhydrobiose depuis un quart de siècle: Critères cytologiques d' aptitude à la reviviscence de thallus de *Riccia macrocarpa* Lev. [Reviviscence of a bryophyte in anhydrobiosis for a quarter of a century: Cytological criteria of reviviscence ability in *Riccia macrocarpa* Lev. thalli.]. Compt. Rend. Acad. Sci. (Paris) Ser. III Sci. Vie 317: 245-252.

Bristol, B. M. 1916. On the remarkable retention of vitality in moss protonema. New Phytol. 15: 137–143.

Carvalho, R. C. de, Branquinho, C., and Silva, J. M. da. 2011. Physiological consequences of desiccation in the aquatic bryophyte *Fontinalis antipyretica*. Planta 234: 195-205.

Carvalho, R. C. de, Catalá, M., Silva, J. M. da, Branquinho, C., and Barreno, E. 2012. The impact of dehydration rate on the production and cellular location of reactive oxygen species in an aquatic moss. Ann. Bot. 110: 1007-1016.

Clausen, E. 1952. Hepatics and humidity, a study of the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. Dansk Bot. Ark. 15: 5-80.

Clymo, R. S. and Duckett, J. G. 1986. Regeneration of *Sphagnum*. New Phytol. 102: 589-614.

Cruz de Carvalho, R., Bernades da Silva, A., Branquinho, C., and Marques da Silva, J. 2015. Influence of dehydration rate on cell sucrose and water relations parameters in an inducible desiccation tolerant aquatic bryophyte. Environ. Exper. Bot. 120: 18-22.

Csintalan, Z., Proctor, M. C. F., and Tuba, Z. 1999. Chlorophyll fluorescence during drying and rehydration in the mosses *Rhytidiadelphus loreus* (Hedw.) Warnst., *Anomodon viticulosus* (Hedw.) Hook. and Tayl. and *Grimmia pulvinata* (Hedw.) Sm. Ann. Bot. 84: 235-244.

Csintalan, Z., Takács, Z., Proctor, M. C., Nagy, Z., and Tuba, Z. 2000. Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland. Plant Ecol. 151: 51-54.

Davey, M. C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25-31.

Deltoro, V. I., Calatayud, A., Gimeno, C., and Barreno, E. 1998a. Water relations, chlorophyll fluorescence, and membrane permeability during desiccation in bryophytes from xeric, mesic, and hydric environments. Can. J. Bot. 76: 1923-1929.

Deltoro, V. I., Calatayud, A., Gimeno, C., Abadia, A., and Barreno, E. 1998b. Changes in chlorophyll a fluorescence, photosynthetic CO_2 assimilation and xanthophyll cycle interconversions during dehydration in desiccation-tolerant and intolerant liverworts. Planta 207: 224-228.

Dhindsa, R. S. 1985. Non-autotrophic CO_2 fixation and drought tolerance in mosses. J. Exper. Bot. 36: 980-988.

Dhindsa, R. S. and Bewley, J. D. 1978. Messenger RNA is conserved during drying of the drought-tolerant moss *Tortula ruralis*. Proc. Nat. Acad. Sci. USA 75: 842-846.

Dilks, T. J. K. and Proctor, M.C.F. 1974. The pattern of recovery of bryophytes after desiccation. J. Bryol. 8: 97-115.

Dilks, T. J. K. and Proctor, M. C. F. 1976a. Seasonal variation in desiccation tolerance in some British bryophytes. J. Bryol. 9: 239-247.

Dilks, T. J. K. and Proctor, M. C. F. 1976b. Effects of intermittent desiccation on bryophytes. J. Bryol. 9: 249-264.

Egunyomi, A. 1979. Autecology of *Octoblepharum albidum* in western Nigeria. II. Phenology and water relations. Nova Hedw. 31: 377-389.

Farrar, J. F. and Smith, D. C. 1976. Ecological physiology of the lichen *Hypogymnia physodes*. III. The importance of the rewetting phase. New Phytol. 77: 93-103.

Glime, J. M. 2015. Water relations: Physiological adaptations. Ch. 7-5, and Ecophysiology of Development: Spore germination. Ch. 5-2. In: Glime, J. M. Bryophyte Ecology. Vol. 1. Physiological ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 5 May 2015 and [accessed 15 July 2015]. Available at <www.bryoecol.mtu.edu>.

Greenwood, J. L. and Stark, L. R. 2014. The rate of drying determines the extent of desiccation tolerance in *Physcomitrella patens*. Funct. Plant Biol. 41: 460-467.

Gupta, R. K. 1977a A study of photosynthesis and leakage of solutes in relation to the desiccation effects in bryophytes. Can. J. Bot. 55: 1186-1194.

Gupta, R. K. 1977b An artefact in studies of the responses of respiration of bryophytes to desiccation. Can. J. Bot. 55: 1195-1200.

Guschina, I. A., Harwood, J. L., Smith, M., Beckett, R. P. 2002. Abscisic acid modifies the changes in lipids brought about by water stress in the moss *Atrichum androgynum*. New Phytol. 156: 255-264.

Hamerlynck, E., Tuba, Z., Csintalan, Z., Nagy, Z., Henebry, G., and Goodin, D. 2000. Diurnal variation in photochemical dynamics and surface reflectance of the desiccation-tolerant moss, *Tortula ruralis*. Plant Ecol. 151: 55-63.

Hamerlynck, E. I., Csintalan, Z., Nagy, Z., Tuba, Z., Goodin, D, and Henebry, G. I. 2002. Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss *Tortula ruralis*. Oecologia 131: 498-505.

Hanslin, H. M., Bakken, S., and Pedersen, B. 2001. The impact of watering regime and ambient relative humidity on the effect of density on growth in two boreal forest mosses, *Dicranum majus* and *Rhytidiadelphus loreus*. J. Bryol. 23: 43-54.

Heddad, M. and Adamska, I. 2002. The evolution of light stress proteins in photosynthetic organisms. Compar. Funct. Genomics 3: 504-510.

Hinshiri, H. M. and Proctor, M. C. F. 1971. The effect of desiccation on subsequent assimilation and respiration of the bryophytes *Anomodon viticulosus* and *Porella platyphylla*. New Phytol. 70: 527-738.

Hoekstra, F. A. 2005. Differential longevities in desiccated anhydrobiotic plant systems. Integrat. Compar. Biol. 45: 725-733.

Hosokawa, T. and Kubota, H. 1957. On the osmotic pressure and resistance to desiccation of epiphytic mosses from a beech forest, south-west Japan. J. Ecol. 45: 579-591.

Hutin, C., Nussaume, L., Moise, N., Moya, I., Kloppstech, K., and Havaux, M. 2003. Early light-induced proteins protect *Arabidopsis* from photooxidative stress. Proc. Natl. Acad. Sci. 100: 4921-4926.

Iljin, W. S. 1953. Causes of death of plants as a consequence of loss of water: Conservation of life in desiccated tissue. Bull. Torrey Bot. Club 80: 166-167.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8: 257-274.

Keever, C. 1957. Establishment of *Grimmia laevigata* on bare granite. Ecology 38: 422-429.

Košnar, J. and Kolář, F. 2009. A taxonomic study of selected European taxa of the *Tortula muralis* (Pottiaceae, Musci) complex: Variation in morphology and ploidy level. Preslia 81: 399-421.

Koster, K. L., Balsamo, R. A., Espinoza, C., and Oliver, M. J. 2010. Desiccation sensitivity and tolerance in the moss *Physomitrella patens*: Assessing limits and damage. Plant Growth Reg. 62: 293-302.

Kranner, I., Beckett, R. P., Wornik, S., Zorn, M., and Pfeifhofer, H. W. 2002. Revival of a resurrection plant correlates with its antioxidant status. Plant J. 31: 13-24.

Krochko, J. E., Bewley, J. D., and Pacey, J. 1978. The effects of rapid and very slow speeds of drying on the ultrastructure and metabolism of the desiccation-sensitive moss *Cratoneuron filicinum* (Hedw.) Spruce. J. Exper. Bot. 29: 905-917.

Krochko, J. E., Winner, W. E., and Bewley, J. D. 1979. Respiration in relation to adenosine triphosphate content during desiccation and rehydration of a desiccation-tolerant and a desiccation-intolerant moss. Plant Physiol. 64: 13-17.

Larson, D. W. 1981. Differential wetting in some lichens and mosses: The role of morphology. Bryologist 84: 1-15.

Li, Y., Wang, Z.-B., Xu, T.-H., Tu, W.-F., Liu, C., Zhang, Y.-M., and Yang, C.-H. 2010. Reorganization of photosystem II is involved in the rapid photosynthetic recovery of desert moss *Syntrichia caninervis* upon rehydration. J. Plant Physiol. 167: 1390-1397.

Longton, R. E. and Schuster, R. M. 1983. Reproductive biology. In: Schuster, R. M. (ed.). New Manual of Bryology, Vol. 1. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan, pp. 386-462.

Lüttge, U., Meirelles, S. T., and De Mattos, E. A. 2008. Strong quenching of chlorophyll fluorescence in the desiccated state in three poikilohydric and homoiochlorophyllous moss species indicates photo-oxidative protection on highly light-exposed rocks of a tropical inselberg. J. Plant Physiol. 165: 172-181.

Maheu, J. 1922. Régénération du *Barbula ruralis* après quatorze ans de sécheresse par protonémas foliaires primaires propagulifères et protonémas secondaires bulbigènes. Bull. Soc. Bot France 69: 330-334.

Makinde, A. M. 1993. Thermotolerance of selected mosses of southwestern Nigeria savanna. Nigerian J. Bot. 6: 21-25.

Makinde, A. and Fajuke, A. A. 2009. Adaptive strategies of mosses to desiccation. Not. Bot. Horti Agrobot. Cluj-Napoca 37: 191-193.

Malta, N. 1921. Versuch über die Widerstandsfähigkeit der Moose gegen Austroeknung. Acta Univ. Latv. 1: 125-129.

Manukjanová, A., Štechová, T., and Kučera, J. 2014. Drought survival test of eight fen moss species. Cryptog. Bryol. 35: 397-403.

Marschall, M. and Proctor, M. C. F. 1999. Desiccation tolerance and recovery of the leafy liverwort *Porella platyphylla* (L.) Pfeiff.: Chlorophyll-fluorescence measurements. J. Bryol. 21: 257-262.

Melick, D. R. and Seppelt, R. D. 1992. Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. Antarct. Sci. 4: 399-404.

Melick, D. R. and Seppelt, R. D. 1994. Seasonal investigations of soluble carbohydrates and pigment levels in Antarctic bryophytes and lichens. Bryologist 97: 13-19.

Minibayeva, F. and Beckett, R. P. 2001. High rates of extracellular superoxide production in bryophytes and lichens, and an oxidative burst in response to rehydration following desiccation. New Phytol. 152: 333-341.

Mishler, B. D. and Newton, A. E. 1988. Influences of mature plants and desiccation on germination of spores and gametophytic fragments of *Tortula*. J. Bryol. 15: 327-342.

Moore, J. P., Le, N. T., Brandt, W. F., Driouich, A., and Farrant, J. M. 2009. Towards a systems-based understanding of plant desiccation tolerance. Trends Plant Sci. 14: 110-117.

Moore, C. J., Luff, S. E., and Hallam, N. D. 1982. Fine structure and physiology of the desiccation-tolerant mosses, *Barbula torquata* Tayl. and *Triquetrella papillata* (Hook. F. and Wils.) Broth., during desiccation and rehydration. Bot. Gaz. 143: 358-367.

Neale, A. D., Blomstedt, C. K., Bronson, P., Le, T. N., Guthridge, K., Evans, J., Gaff, D. F., and Hamill, J. D. 2000. The isolation of genes from the resurrection grass *Sporobolus stapfianus* which are induced during severe drought stress. Plant Cell Environ. 23: 265-277.

Noailles, M. 1978. Etude ultrastructurale de la récupération hydrique aprè une période de sècheresse chez une Hypnobryale: *Pleurozium schreberi* (Willd.) Mitt. Ann. Sci. at. Ser. 12: 19, 249-265.

Ochi, H. 1952. The preliminary report on the osmotic value, permeability, drought and cold resistance of mosses. Bot. Mag. Tokyo 65: 10-12.

O'Mahony, P. J. and Oliver, M. J. 1999. The involvement of ubiquitin in vegetative desiccation tolerance. Plant Molec. Biol. 41: 657-667.

Oliver, M. J. 1991. Influence of protoplasmic water loss on the control of protein synthesis in the desiccation-tolerant moss *Tortula ruralis*. Plant Physiol. 97: 1501-1511.

Oliver, M. J. 1996. Desiccation tolerance in vegetative plant cells. Physiol. Plant. 97: 779-787.

Oliver, M. J. and Bewley, J. D. 1984a. Plant desiccation and protein synthesis. IV. RNA synthesis, stability, and recruitment of RNA into protein synthesis during desiccation and rehydration of the desiccation-tolerant moss, *Tortula ruralis*. Plant Physiol. 74: 21-25.

Oliver, M. J. and Bewley, J. D. 1984b. Desiccation and ultrastructure in bryophytes. Adv. Bryol. 2: 91-131.

Oliver, M. J., Mishler, B. D., and Quisenberry, J. E. 1993. Comparative measures of desiccation-tolerance in the *Tortula ruralis* complex. I. Variation in damage control and repair. Amer. J. Bot. 80: 127-136.

Oliver, M. J., Wood, A. J., and O'Mahony, P. 1997. How some plants recover from vegetative desiccation: A repair based strategy. Acta Physiol. Plant. 19: 419-425.

Oliver, M. J., Velten, J., and Mishler, B. D. 2005. Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats? Integr. Compar. Biol. 45: 788-799.

Patterson, P. M. 1964. Problems presented by bryophytism. Bryologist 67: 390-396.

Peterson, G., Moyá, M. T., Zotz, G., Goslin, M., Kay, A., Maple, M., and Reich, A. 1994. Estimation of water loss rates in epiphytes. Trop. Biol.: Ecol. Appr. 94: 35-37.

Peterson, W. L. and Mayo, J. M. 1975. Moisture stress and its effect on photosynthesis in *Dicranum polysetum*. Can. J. Bot. 53: 2897-2900.

Pressel, S. 2006. Effects of de- and rehydration on food-conducting cells in the moss *Polytrichum formosum*: A cytological study. Ann. Bot. 98: 67-76.

Pressel, S. and Duckett, J. G. 2010. Cytological insights into the desiccation biology of a model system: Moss protonemata. New Phytol. 185: 944-963.

Proctor, M. C. F. 1981. Physiological ecology of bryophytes. Adv. Bryol. 1: 79-166.

Proctor, M. C. F. 2000b. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Proctor, M. C. F. 2001. Patterns of desiccation tolerance and recovery in bryophytes. Plant Growth Reg. 35(2): 147-156.

Proctor, M. C. F. 2003. Experiments on the effect of different intensities of desiccation on bryophyte survival, using chlorophyll fluorescence as an index of recovery. J. Bryol. 25: 201-210.

Proctor, M. C. and Smirnoff, N. 2000. Rapid recovery of photosystems on rewetting desiccation-tolerant mosses: Chlorophyll fluorescence and inhibitor experiments. J. Exper. Bot. 51: 1695-1704.

Proctor, M. C. F., Ligrone, R., and Duckett, J. G. 2007. Desiccation tolerance in the moss *Polytrichum formosum*: Physiological and fine-structural changes during desiccation and recovery. Ann. Bot. 99: 75-93.

Richardson, D. H. S. 1981. The Biology of Mosses. Blackwell Scientific Publications, London.

Richardson, D. H. S. and Nieboer, J. E. 1980. Surface binding and accumulation of metals in lichens. In: Cook, C. B., Pappas, P. W., and Rudolph, E. D. (eds.): Cellular Interactions in Symbiotic and Parasitic Associations. 5th Ann. Colloq. Coll. Biol. Sci., Ohio State Univ. Press, pp. 75-94.

Sagot, C. and Rochefort, L. 1996. Tolerance des Sphaignes a la desiccation. Cryptog. Bryol. Lichenol 17: 171-183.

Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140: 677-684.

Schonbeck, M. W. and Bewley, J. D. 1981a. Responses of the moss *Tortula ruralis* to desiccation treatments. I. Effects of minimum water content and rates of dehydration and rehydration. Can. J. Bot. 59: 2698-2706.

Schonbeck, M. W. and Bewley, J. D. 1981b. Responses of the moss *Tortula ruralis* to desiccation treatments. II. Variations in desiccation tolerance. Can. J. Bot. 59: 2707-2712.

Segreto, R., Hassel, K., Bardal, R., and Stenøien, H. K. 2010. Desiccation tolerance and natural cold acclimation allow cryopreservation of bryophytes without pretreatment or use of cryoprotectants. Bryologist 113: 760-769.

Singh, J., Blackwell, B., Miller, R., and Bewley, D. 1984. Membrane organization of the desiccation tolerant moss *Tortula ruralis* in several dehydrated states. Abstracts, Annual Meeting of the American Society of Plant Physiologists, 12-17 Aug., 1984. Univ. Calif. – Davis, p. 31.

Sollows, M. C., Frego, K. A., and Norfolk, C. 2001. Recovery of *Bazzania trilobata* following desiccation. Bryologist 104: 421-429.

Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.

Stark, L. R., Greenwood, J. L., Brinda, J. C., and Oliver, M. J. 2013. The desert moss *Pterygoneurum lamellatum* (Pottiaceae) exhibits an inducible ecological strategy of desiccation tolerance: Effects of rate of drying on shoot damage and regeneration. Amer. J. Bot. 100: 1522-1531.

Stark, L. R., Greenwood, J. L., and Brinda, J. C. 2016. Desiccated *Syntrichia ruralis* shoots regenerate after 20 years in the herbarium. J. Bryol. (in press).

Streusand, V. J. and Ikuma, H. 1986. Desiccation tolerance in mosses. I. Development of a method for measuring cell damage. Can. J. Bot. 64: 2388-2392.

Stewart, G. R. and Lee, J. R. 1972. Desiccation injury in mosses. II. The effects of moisture stress on enzyme levels. New Phytol. 71: 461-466.

Trebacz, K., Simonis, W., and Schönknecht, G. 1994. Cytoplasmic Ca^{2+}, K^{+}, Cl^{-} and NO_3^{-} activities in the liverwort *Conocephalum conicum* L. at rest and during action potentials. Plant Physiol. 106: 1073-1084.

Vanderpoorten, A. and Goffinet, B. 2009. Introduction to Bryophytes. Cambridge University Press, Cambridge.

Volk, O. H. 1984. Beitrage zur Kenntnis der Marchantiales in Südwest-Afrika/Namibia. IV. Zur Biologie einiger Hepaticae mit besonderer Berücksichtigung der Gattung Riccia. Nova Hedw. 39: 117-143.

Whitehouse, H. L. K. 1984. Survival of a moss, probably *Dicranella staphylina*, in soil stored for nearly 50 years. J. Bryol. 13: 131-133.

Wilson, J. A. and Coxson, D. S. 1999. Carbon flux in a subalpine spruce-fir forest: Pulse release from *Hylocomium splendens* feather-moss mats. Can. J. Bot. 77: 564-569.

Wood, A. J. and Oliver, M. J. 1999. Translational control in plant stress: The formation of messenger ribonucleoprotein particles (mRNPs) in response to desiccation of *Tortula ruralis* gametophytes. Plant J. 18: 359-370.

Wood, A. J., Duff, R. J., and Oliver, M. J. 1999. Expressed sequence tags (ESTs) from desiccated *Tortula ruralis* identify a large number of novel plant genes. Plant Cell Physiol. 40: 361-368.

Wu, N., Zhang, Y.-M., Downing, A., Aanderud, Z. T., Tao, Y., and Williams, S. 2013. Rapid adjustment of leaf angle explains how the desert moss, *Syntrichia caninervis*, copes with multiple resource limitations during rehydration. Funct. Plant Biol. 41: 168-177.

Zeng, Q. and Wood, A. J. 2000. A cDNA encoding ribosomal protein RPL15 from the desiccation-tolerant bryophyte *Tortula ruralis*: mRNA transcripts are stably maintained in desiccated and rehydrated gametophytes. Biosci. Biotechnol. Biochem. 64: 2221-2224.

Zeng, Q., Chen, X., and Wood, A. J. 2002. Two early light-inducible protein (ELIP) cDNAs from the resurrection plant *Tortula ruralis* are differentially expressed in response to desiccation, rehydration, salinity, and high light. J. Exper. Bot. 53: 1197-1205.

Zhang, J., Zhang, Y.-M., Downing, A., Wu, N., and Zhang, B.-C. 2011. Photosynthetic and cytological recovery on remoistening *Syntrichia caninervis* Mitt., a desiccation-tolerant moss from Northwestern China. Photosynthetica 49: 13-20.

CHAPTER 7-7

WATER RELATIONS: BIOCHEMICAL ADAPTATIONS TO DRYING

TABLE OF CONTENTS

Membrane Chemistry 7-7-2
ABA Role 7-7-3
Protection from Oxidation 7-7-6
    Oxidative Damage 7-7-6
    Glutathione 7-7-8
    Pathogen Danger 7-7-9
Shoot Tips – Variable Tolerance within Plants 7-7-10
The Genes 7-7-10
Summary 7-7-11
Acknowledgments 7-7-11
Literature Cited 7-7-11

CHAPTER 7-7

WATER RELATIONS: BIOCHEMICAL ADAPTATIONS TO DRYING

Figure 1. ***Grimmia affinis*** drying on a rock. Photo by Michael Lüth, with permission.

The biochemistry of bryophytes is still a relatively young field. This is true of the biochemical level of response of bryophytes to desiccation stress. This chapter will attempt to portray what we know and how that biochemistry relates to the habitats of the bryophytes. But at this early stage in our studies, few species have been studied in detail, leaving much of the discussion incomplete or even somewhat ambiguous.

Membrane Chemistry

Since membrane damage is a common response to desiccation stress, Guschina *et al*. (2002) examined lipid composition of membranes in ***Atrichum androgynum*** (Figure 19) during desiccation in an effort to understand the role of the stress hormone **ABA**. Drought stress causes changes in the phosphoglyceride composition of the membranes. Reduction of thylakoid lipids, resulting in chlorophyll damage, causes a loss in photosynthesis as a result of desiccation, as already demonstrated in tracheophytes. Guschina *et al*. found that application of ABA reduced the extent of these membrane lipid changes.

Some plants may take advantage of the leakage through damaged membranes to rid cells of protectants used during dehydration. Working with canopy liverworts in the tropical rainforest of Guadeloupe, Coxson and coworkers (1992) found that for ***Frullania atrata***, exposure to simulated wetting/drying resulted in production of substantial glucose, erythritol, glycerol, and sucrose. They suggest that whereas these sugars may help this liverwort survive severe desiccation, the liverwort subsequently releases them into throughfall upon rewetting.

Robinson *et al*. (2000) suggest that sugars may indeed help some mosses survive desiccation. They found stachyose, an oligosaccharide known for its role in desiccation tolerance of seeds, in ***Bryum pseudotriquetrum*** (Figure 2), but not in ***Ceratodon purpureus*** (Figure 3; most tolerant) or ***Schistidium antarctici*** (Figure 4; least tolerant). This is another example showing that not all bryophytes have the same adaptations to desiccation.

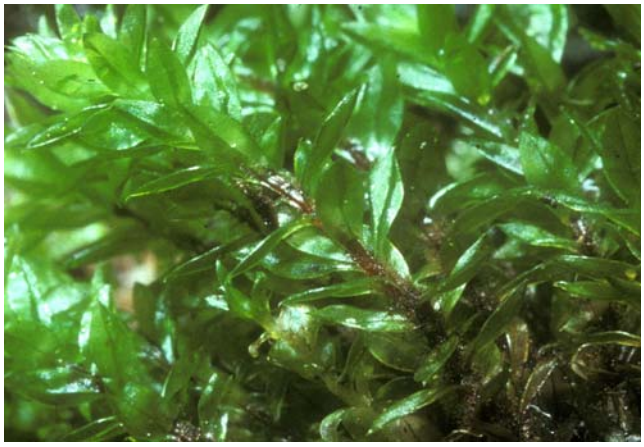

Figure 2. ***Bryum pseudotriquetrum***, a moss in which the sugar stachyose aids in desiccation tolerance. Photo by Janice Glime

Figure 3. ***Ceratodon purpureus***, a moss that does not use stachyose to aid in desiccation tolerance. Photo by Janice Glime.

Figure 4. Drought-intolerant ***Schistidium antarctici*** on Macquarie Island. Photo by Rod Seppelt, with permission.

ABA Role

The stress hormone **ABA** (abscisic acid) is present in many groups of organisms, including animals and bacteria as well as plants (Hartung 2010; Takezawa *et al*. 2011). This ability to protect against abiotic stress may have been one of the most critical attributes permitting plants to move to land.

Using immunoassay, Hartung and coworkers (1987, 1994) demonstrated the presence of ABA in all **Bryopsida**, **Anthocerotophyta**, and **Marchantiopsida** tested. They were able to extract more ABA from the hornwort ***Phaeoceros*** grown under slightly drier areas than from those in wetter areas. Furthermore, they have shown that the sporophyte of ***Phaeoceros laevis*** (Figure 5) produces ABA in response to stress and that the sporophyte guard cells close in response to ABA, much as in tracheophytes. This is in sharp contrast to the findings of Duckett and Ligrone (2004). They were unable to find any response to ABA or to moisture changes in the stomata of ***Phaeoceros***.

Figure 5. ***Phaeoceros laevis*** sporophytes, a hornwort with stomata in the capsule. Photo by Robert Klips, with permission.

In bryophytes, this hormone occurs in ***Physcomitrella patens*** (Figure 6) where it has a major role in dehydration stress tolerance (Takezawa *et al*. 2011). To determine the genetic response of bryophytes to water stress, Cuming *et al*. (2007) used the lab moss ***Physcomitrella patens***. These plants were subjected to ABA as well as osmotic, salt, and drought stress. The response of the protonema differed from that of the gametophore, with 130 genes in the protonema responding to dehydration. Of these, 56 were induced by ABA, but only 10 genes by osmotic stress and 8 by salt stress. Another 51 genes were induced by more than one of these treatments. Many of the ABA and drought-responsive genes were homologues of those expressed during seed development, supporting the assertions of Fisher (2008) discussed in Chapter 7-5. As seen by Wang *et al*. (2009) during dehydration, many of the ABA- and drought-responsive genes include genes for **LEA proteins**.

Figure 6. ***Physcomitrella patens***, a moss in which ABA increases stress tolerance. Photo by Michael Lüth, with permission.

Werner *et al*. (1991) found that even protonemata produce ABA in response to slow drying, as shown in ***Funaria hygrometrica***, and as in mature plants, it imparts drought tolerance. But it does not inhibit water loss. Rather, it appears to induce synthesis of new proteins that impart drought tolerance.

In Cyanobacteria and algae, the few studies on stress-induced ABA production indicate that the excess is released to the external medium (Hartung 2010). Taking an evolutionary approach, Hartung demonstrated that organisms that start to colonize terrestrial habitats increase their ABA production in response to even mild drought stress. Such signals seem to initiate the production of terrestrial organs, perhaps explaining the change from aquatic to terrestrial forms of ***Riccia fluitans*** (Figure 7; see below). In bryophytes, stomata respond to ABA. The levels of ABA in sporophytes of hornworts and mosses that have stomata is especially high, although the regulatory role of the ABA seems ambiguous. Fungi release ABA, and these hormones may interact with the bryophytes through mycorrhizal associations or just through their presence in the environment.

Figure 7. ***Riccia fluitans***, exposed here to air drying. ABA can facilitate conversion to the wider terrestrial form. Photo by Jan-Peter Frahm, with permission.

One of the unusual abilities of ABA is to cause the conversion of the aquatic forms of the thallose liverworts ***Riccia fluitans*** (Figure 7) and ***Ricciocarpos natans*** (Figure 8) into their terrestrial forms (Hellwege *et al.* 1992; Hartung *et al*. 1994). This conversion results in plants with greater volume, hence a smaller surface area to volume ratio, making them somewhat less vulnerable to desiccation.

Liverworts use **lunularic acid** where other plants use ABA as a dormancy hormone and, apparently, to help prepare them for drying, as shown in ***Lunularia cruciata*** (Figure 9) (Schwabe 1990). When subjected to long days, their drought resistance increases (Figure 10), as does their lunularic acid content.

Figure 8. ***Ricciocarpos natans***, stranded here out of water. ABA can facilitate conversion to the terrestrial form. Photo by Janice Glime.

Figure 9. ***Lunularia cruciata***, a thallose liverwort that produces the ABA-like lunularic acid as a dormancy hormone. Photo by Michael Lüth, with permission.

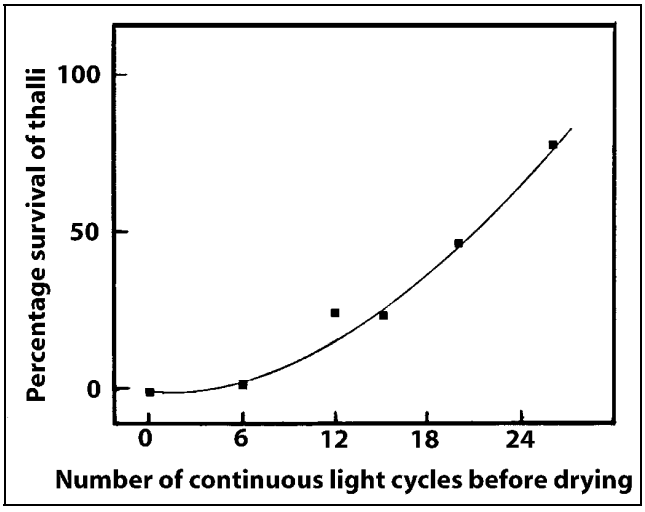

Figure 10. Effect of long-day (continuous) light on induction of drought resistance, resulting in drought survival in the thallose liverwort ***Lunularia cruciata***. Based on Schwabe (1990).

Although the presence of lunularic acid seems to be universal in liverworts, and has functions like those of

ABA, liverworts seem to be fully responsive to ABA. Pence (1998) found that ABA was necessary for the cryopreservation of some liverworts such as ***Riccia fluitans*** (Figure 7) and ***Marchantia polymorpha*** (Figure 21), preventing desiccation damage, but it had little effect on the leafy liverwort ***Plagiochila*** (Figure 11).

Burch and Wilkinson (2002) used ABA and sucrose to increase the success of cryopreservation of the moss ***Ditrichum cornubicum*** (Figure 12) protonemata. We also know that application of ABA increases the desiccation tolerance of the mesophytic moss ***Atrichum undulatum*** (Figure 13) (Beckett *et al*. 2000). Using ***Atrichum androgynum*** (Figure 19), Guschina *et al*. (2002) demonstrated phosphoglyceride composition changes during water stress. ABA treatment reduces the overall extent of these changes, possibly by reducing membrane damage by reducing the lipid changes.

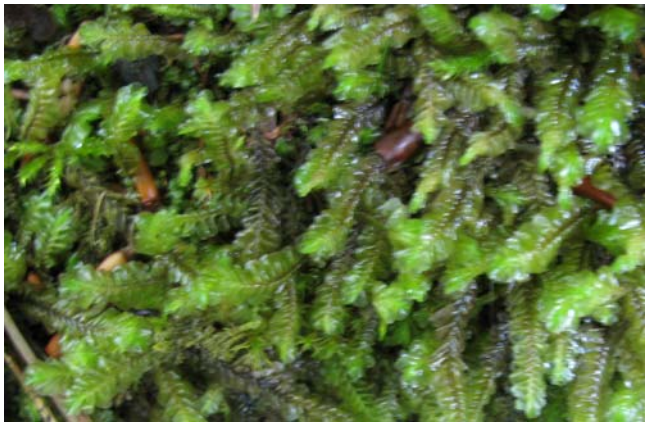

Figure 11. ***Plagiochila asplenioides*** near a stream in Wales. Photo by Janice Glime.

Figure 12. ***Ditrichum cornubicum***, a moss that survives cryopreservation with the help of ABA and sucrose. Photo by David T. Holyoak, with permission.

The Afromontane understory moss ***Atrichum androgynum*** (Figure 19) recovers its CO_2 fixation more slowly than recovery of photosystem II activity following 16 hours of desiccation, then rehydration (Mayaba *et al*. 2001). Pretreatment with ABA increases the recovery rate of both of these activities and doubles the non-photochemical quenching, hence reducing reactive oxygen species. Mayaba and coworkers suggest that this may partly explain the desiccation hardening process in this species. Plants pretreated with ABA, unlike untreated plants, experience a significant increase in soluble sugars that could promote the vitrification (transformation into a glassy substance) of the cytoplasm. This could, in turn, protect the membranes during desiccation. ABA has only a slight effect on the starch concentrations during desiccation. ABA furthermore has no effect on chlorophyll breakdown.

Figure 13. ***Atrichum undulatum*** showing some plants drying and curling. This moss changes its phosphoglyceride composition during drought stress. Photo by Janice Glime.

But how does this relate to preventing the oxidative damage? Beckett and coworkers (2000) suggested that ABA pretreatment may act by reducing the energy transfer between light-harvesting chlorophyll II and photosystem II. This could harden the moss to desiccation stress by reducing the production of reactive oxygen at the site of photosystem II. Experiments indicated that photosystem II photosynthesis recovers faster in the pre-treated plants.

ABA may play another role as well. One of the most serious consequences of desiccation is loss of membrane integrity, causing membranes to become leaky (Bewley 1979). Beckett (1999) found that application of ABA could reduce the loss of K^+ from ***Atrichum androgynum*** (Figure 19) in much the same manner as partial dehydration treatment prior to desiccation. The response is similar to that obtained by reducing the relative water content to 0.6 for three days, which reduces the K^+ loss by 15-20%. This seems to be the ideal combination because using less humid air or more time does not decrease the K^+ loss further. This species, and probably most, experiences **drought hardening** (process of increasing resistance to drought; see Chapter 7-5) as the dry season progresses, as indicated by the loss of 80% of its intracellular K^+ at the beginning of the dry season, but less than 25% by the end of that season (Beckett & Hoddinott 1997).

Abscisic acid (ABA) has already been noted to have an important role in desiccation tolerance. Werner *et al*. (1991) found that slowly dried protonemata of ***Funaria hygrometrica*** survived desiccation, but rapidly ones did not. The slowly dried mosses experienced a six-fold increase in abscisic acid during drying. If ABA is added to the protonemata at an appropriate concentration, the ABA mediates drought tolerance, apparently by inducing the synthesis of new proteins.

Sucrose

De Cruz *et al*. (2014, 2015) found that desiccated cells of the aquatic moss ***Fontinalis antipyretica*** lose 50% of their sucrose through leakage when the cells are rehydrated. Fast dehydration results in higher sucrose accumulation, but it is not enough to induce desiccation tolerance. The increase in soluble sugars helps in osmoregulation during the decreasing turgor pressure of the cells. In addition to serving as an osmolyte, sucrose in bryophytes helps to stabilize membranes and proteins through **vitrification** (process of forming glasslike substances). In ***Fontinalis antipyretica*** desiccation tolerance requires slow dehydration, suggesting that high sucrose content does not act alone to create desiccation tolerance.

Protection from Oxidation

Just what is it that varies among the bryophytes that dry out, become metabolically inactive, and then revive? What physiological mechanism protects, or fails to protect them? How can photosynthesis achieve its maximum rate within 30 seconds upon receiving rain or dew in some desiccated species (Anderson 1980)? Proctor (1990) and Alpert (2000) suggest that in drought-hardening the cell must protect itself from oxidative damage, as well as loss of configuration of macromolecules, and this protection depends on the intensity and duration of desiccation.

Minibayeva and Beckett (2001) noted that drought-sensitive bryophytes can release an **oxidative burst** (respiratory burst; rapid release of reactive oxygen species – superoxide radical and hydrogen peroxide) in response to rehydration. These bursts developed best in the hornwort and two thalloid liverworts tested (Minibayeva & Beckett 2001). A similar oxygen burst is, however, almost absent in all the mosses tested as well as a leafy liverwort and desiccation-tolerant lichens.

Oxidative Damage

Kramer *et al*. (2002) examined the "resurrection plants" – those plants that can survive desiccation – to determine what permits them to survive. They found that in a woody plant desiccation can trigger increases in zeaxanthin and redox shifts of the antioxidants glutathione and ascorbate to their oxidized forms. New ascorbate and glutathione were produced upon rehydration and the oxidized forms from the dehydration event changed back to reduced forms. Using lichens, Kramer *et al*. (2008) further demonstrated that reactive oxygen species can damage nearly every molecule in living cells. These included nucleic acids, proteins, and lipids.

The absence of oxidative bursts in mosses lends support to the hypothesis that mosses protect themselves from the damage such highly reactive oxidative bursts can cause during rehydration. Shiono *et al*. (2000) found that in testing the liverwort ***Marchantia paleacea*** subsp. ***diptera*** (Figure 15), the moss ***Barbula unguiculata*** (Figure 16), and the hornwort ***Anthoceros punctatus*** (Figure 17), the liverwort differed from the other two in its isozyme patterns for **superoxide dismutase**. This enzyme is known for its ability to maintain safe levels of the highly reactive oxides that are produced during cell stress, including effects of desiccation.

Figure 14. ***Physcomitrella patens***, a species that exhibits oxidative bursts in response to a fungal presence. Photo by Michael Lüth, with permission.

Minibayeva and Beckett (2001) conclude that patterns of oxide production are correlated with the moisture status of the habitat. Those species with high basal rates of oxide production grow in moist microhabitats, have a moderately high thallus water content, have high K^+ contents, and have well developed oxidative bursts. Species with such oxidative bursts also lose a high proportion of their intracellular K^+ (55-98% in liverworts and hornworts) upon rehydration. Mosses and the one leafy liverwort were all collected from wet habitats and all produced oxides at low rates compared to the thallose liverworts and hornworts.

Figure 15. ***Marchantia palacea*** subsp. ***diptera*** from Japan. Photo by Janice Glime.

The aquatic moss ***Fontinalis antipyretica*** (Figure 18) exhibits the potential danger of high oxygen levels. De Carvalho *et al*. (2012) demonstrated that under slow dehydration, this species exhibits low production of reactive oxygen species upon rehydration, a phenomenon that reduces the cellular damage and increases cell survival. The slow drying apparently reduces the oxidative burst by limiting production of reactive oxygen species.

Figure 16. ***Barbula unguiculata*** dry, retaining its green color that permits it to respond quickly to rehydration. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 17. ***Anthoceros punctatus***, a hornwort having similar isozyme patterns to those of the moss ***Barbula unguiculata***. Photo by Jonathan Sleath, with permission.

Figure 18. ***Fontinalis antipyretica*** in dry stream. Photo by Janice Glime.

But some bryophytes produce high quantities of oxides even when they are not stressed, and some bryophytes produce them at extremely high rates. For example, ***Anthoceros natalensis*** exceeds 1000 µmol g^{-1} dry mass h^{-1}, whereas excised tracheophyte roots produce only about 1% of that amount (Minibayeva *et al*. 1998). These data do not present a consistent pattern that permits us to interpret the role of oxidative bursts or superoxide dismutase in protecting bryophyte cells that undergo desiccation. Instead, the high oxidative responses in some species may be one to the presence of invading pathogens (see below).

Mayaba *et al*. (2002) later found that ***Atrichum androgynum*** (Figure 19) from the Afromontane understory displays an oxidative burst of hydrogen peroxide (H_2O_2), not superoxides, during rehydration, with maximum rates during the first 15 minutes (Figure 20). The moss even produces peroxide during times when dehydration is insufficient to cause K^+ leakage. Using polyethylene glycol to induce desiccation causes the moss to produce significant amounts of H_2O_2. Mayaba and coworkers suggest that peroxidases might be responsible for the production of H_2O_2. They determined that ABA and light influenced the rate of production of peroxide.

Figure 19. ***Atrichum androgynum***, a moss with an oxidative burst, especially during the first 15 minutes of rehydration. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

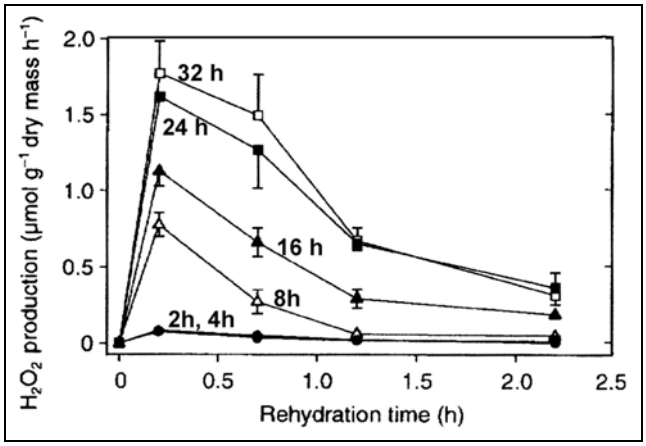

Figure 20. Peroxide (H_2O_2) production during rehydration following various dehydration periods (indicated on each line) in ***Atrichum androgynum*** from KwaZulu-Natal Province, Republic of South Africa, during summer. Vertical bars indicate standard deviation; n=5. Redrawn from Mayaba *et al*. (2002).

This peroxidase system would have several advantages. Peroxidases oxidize phenolics to quinones and generate peroxide (H_2O_2). Peroxide, a well-known antibacterial agent for cleaning cuts and wounds, can itself help to kill invading organisms. Furthermore, peroxide releases free radicals that increase polymerization of phenolics into lignin-like substances. In tracheophytes,

these substances are known to reinforce the cell wall and contain the pathogens. They may have similar roles in bryophytes.

The thallose liverwort ***Marchantia polymorpha*** (Figure 21) contains a peroxidase that has been characterized as a glycoprotein that is different from any known tracheophyte peroxidase (Hirata *et al*. 2000). Hirata and coworkers demonstrated that this peroxidase is able to perform oxidative polymerization of **lunularin**, the liverwort counterpart of ABA.

Figure 21. ***Marchantia polymorpha***, a thallose liverwort that produces a peroxidase with a glycoprotein that differs from those in tracheophytes. Photo by David T. Holyoak, with permission.

Other known constituents also influence the activity of peroxidases. Seel *et al*. (1992a) examined the effects of desiccation on **superoxide dismutase** (enzyme that destroys highly reactive superoxides by converting them into peroxide and O_2) activity in ***Syntrichia ruralis*** var. ***arenicola*** (=*Tortula ruraliformis*; Figure 22), a desiccation-tolerant moss, and ***Dicranella palustris*** (Figure 23), a flush moss with limited desiccation tolerance. Activity of this enzyme is known to enhance membrane integrity (Dhindsa & Matowe 1981; Dhindsa *et al*. 1981; Gong *et al*. 1997). ***Syntrichia ruralis*** var. ***arenicola*** has higher superoxide dismutase activity in both the hydrated and desiccated states than does ***D. palustris*** (Seel *et al*. 1992a). But effects on the activities of peroxidase or ascorbic peroxidase do not seem to be related to hydration state. Nevertheless, both species become depleted of the anti-oxidant ascorbic acid when desiccated. From these experiments, Seel and coworkers deduced that anti-oxidants may be more important than removal of chloroplastic peroxide in endowing desiccation tolerance. Using different methods, Seel and coworkers (1992b) found a greater lipid peroxidation in ***D. palustris*** than in ***S. ruralis*** var. ***arenicola*** following desiccation. Calcium also seems to play a role by increasing superoxide dismutase activity, thus enhancing membrane integrity (Gong *et al*. 1997).

Proctor *et al*. (2007) used the endohydric moss ***Polytrichastrum formosum*** (Figure 30) to try to resolve conflicting implications between physiological and cytological evidence regarding desiccation recovery in bryophytes. They found that protein synthesis inhibitors cause rapid decline of photosynthetic recovery in the light, but not in the dark. Rapid recovery of respiration and photosynthesis indicates that systems are conserved intact during the dehydration and rehydration, an indication that is consistent with the physical evidence that thylakoids and cristae do remain intact during the dehydration-rehydration process. Microbodies that are closely associated with chloroplasts remain unchanged during the dehydration-rehydration process and play an important role in removal of the superoxide radicals (Duckett & Renzaglia 1988; Smirnoff 1993; Minibayeva & Beckett 2001; Mayaba *et al*. 2002). The prominence of these microbodies in leaves of ***Syntrichia ruralis*** (Figure 23) (Robertson 1991) and ***Polytrichastrum formosum*** may be associated with the desiccation tolerance of these two species (Proctor *et al*. 2007).

Figure 22. ***Syntrichia ruralis*** var. ***arenicola***, a desiccation-tolerant moss. Photo by Michael Lüth, with permission.

Figure 23. ***Dicranella palustris*** in flush near Swallow Falls, Wales. This moss has limited desiccation tolerance. Photo by Janice Glime.

Glutathione

Glutathione (GSH) is important in protecting plants from environmental stresses like oxidative stress and pathogens (Bruns *et al*. 2001; Burritt 2008). More recent studies have used glutathione to measure drought stress. Activities of the enzymes glutathione reductase, glutathione peroxidase, and glutathione S-transferase increase during slow drying and likewise during rehydration following rapid drying of the drought-tolerant moss ***Syntrichia ruralis*** (Figure 22) (Dhindsa 1991).

On the other hand, the activity of the enzymes malate dehydrogenase exhibit little change during either dehydration or rehydration. Treatment of the moss tissues with cycloheximide, actinomycin D, or cordycepin suppresses the increased activities of glutathione reductase and glutathione S-transferase, but has a much lower effect on glutathione peroxidase. At the same time, the percentage of total glutathione as oxidized glutathione increases. This increase is correlated positively with levels of lipid peroxidation and solute leakage, but is correlated negatively with the rate of protein synthesis. The oxidized glutathione level serves as a good indicator of oxidation stress and suggests that oxidized glutathione may mediate the drought-stress-induced inhibition of protein synthesis.

In addition to protection from oxidative damage, glutathione may help to protect the bryophyte cells from heavy metal damage following rehydration (Saxena & Saxena 2012). Although it is likely that this benefit has not had any evolutionary selection advantage for very long, current pollution conditions often deposit heavy metals that accumulate while the bryophytes are dry. These could gain entry into the cells along with the resorption of needed cell electrolytes during rehydration and before membrane repair is completed. Bruns *et al*. (2001) have demonstrated a protective detoxification role of glutathione against heavy metals in the aquatic moss ***Fontinalis antipyretica*** (Figure 18), Leinenweber *et al*. (2009) in the terrestrial moss ***Thuidium*** sp. (Figure 24), and Saxena and Saxena (2012) in the moist forest moss ***Sphagnum squarrosum*** (Figure 25).

Figure 24. ***Thuidium tamariscinum***, a species that is able to use glutathione as protection against heavy metals. Photo by Michael Lüth, with permission.

Pathogen Danger

The damaging effects of oxides in the cells leads us to question the advantages that may have kept the oxidative burst in the bryophytes for eons. This may be explained by their role in limiting pathogen invasion and damage.

Cells with damaged membranes resulting from desiccation would be vulnerable to invasion by pathogenic microorganisms. Such oxidative bursts as seen upon rehydration can help to limit the spread of invading pathogens because of oxidation toxicity, as well as inducing expression of defense-related genes. Low and Merida (1996) considered the oxidative bursts in plants to facilitate cross-linking of cell wall proteins, induction of defense-related genes, stimulation of **phytoalexin** (substance produced by plant tissues in response to contact with a parasite and that specifically inhibits growth of that parasite) biosynthesis, and promotion of **hypersensitive response** (HR; mechanism to prevent spread of infection by microbial pathogens, causing rapid death of cells in local region surrounding infection).

Figure 25. ***Sphagnum squarrosum***, a species that is able to use glutathione as protection against heavy metals. Photo by J. C. Schou, with permission.

Gupta (1977) reported the oxidative burst in bryophytes as an "artifact." He found that ***Dicranella palustris*** (Figure 23; a wet-habitat moss) and ***Scapania undulata*** (Figure 26; an aquatic leafy liverwort) had a large number of microorganisms present following dehydration and rehydration. This is a reasonable expectation when membranes are damaged and both electrolytes and organic compounds are able to leak from the cells, especially upon rewetting. Furthermore, the respiratory oxygen uptake increased to about 6X that of controls of ***S. undulata***, 2.5X for ***Dicranella palustris***, and 2X for ***Porella platyphylla*** (Figure 27) and ***Mnium hornum*** (Figure 28). Little increase occurred in ***Syntrichia ruralis*** (Figure 22), the most desiccation-tolerant species. But it appears that the respiratory increases were due to the adhering microorganisms, not to the bryophytes. Such respiratory increase could indicate injury to the bryophytes, but it cannot be a useful tool to measure survivorship or metabolic recovery of the bryophytes. These microorganism growths indicate the potential importance of oxidative bursts that can help to protect the bryophyte cells from invasion from these potentially harmful organisms.

Beckett *et al*. (2004) demonstrated that the liverwort ***Dumortiera hirsuta*** (Figure 29) produced extracellular superoxide at high rates even under normal, unstressed circumstances. Nevertheless, production increased extensively during rehydration, but not during desiccation. It appears that peroxides produce the superoxide, but little H_2O_2 seems to be present in the cell. However, indications are that the concentrations of peroxides are rapidly reduced by the liverwort. Beckett and coworkers likewise suggested a role in protection against bacteria and fungi. Lehtonen *et al*. (2012) verified the importance of such

oxidative bursts in response to a fungal elicitor (chiton) in the moss ***Physcomitrella patens*** (Figure 14).

Figure 26. ***Scapania undulata***, a species in which microbial respiration/oxygen uptake increases by a factor of 6 following rehydration. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Porella platyphylla***, a desiccation-tolerant leafy liverwort on tree bark; a species in which microbial respiration/oxygen uptake increases by a factor of 2 following rehydration. Photo by Michael Lüth, with permission.

Figure 28. ***Mnium hornum***, a species in which microbial respiration/oxygen uptake increases by a factor of 2 following rehydration. Photo by Des Callaghan, with permission.

Figure 29. ***Dumortiera hirsuta***, a thallose liverwort that produces extracellular superoxide at high rates even under normal circumstances. Photo by Michael Lüth, with permission.

White and Torres (2010) suggested that endophytes in plants may protect the plants from oxidative damage by the production of antioxidants, thus possibly protecting them against other forms of stress, including desiccation. It appears that this protective role of endophytes (fungi) has not been explored in bryophytes.

Shoot Tips – Variable Tolerance within Plants

Some moss shoot tips may have a rehydration potential not afforded the rest of the plant. In ***Polytrichastrum formosum*** (Figure 30), desiccation in the shoot tips induces the rapid resorption of starch grains in plastids of the meristematic cells without any major **thylakoid** disorganization (Hallet *et al*. 1987). In the adult leaves, however, the starch grains are preserved. Upon rehydration, the plastid ultrastructure of the apex is entirely restored and new starch inclusions appear in less than 4 hours. Little work has been done to relate the resistance of various parts of the bryophyte plants to differences in biochemistry.

Figure 30. ***Polytrichastrum formosum***, a moss where desiccation of the apices causes rapid resorption of starch grains in plastids of the apical meristematic cells. Photo by Des Callaghan, with permission.

The Genes

While the physiologists are attempting to find substances that affect desiccation tolerance and recovery rates, the geneticists are attempting to identify genes and

the biochemical pathways they affect. Chen and coworkers (2002), working with the desiccation-tolerant model system in ***Syntrichia ruralis*** (Figure 22), found a new polypeptide, known as ALDH21A1, that is less than 30% identical to known ALDH proteins. Data suggest that this new aldehyde dehydrogenase plays an important role in the detoxification of aldehydes generated in response to desiccation and may represent a unique stress tolerance mechanism among eukaryotes. Could it be this aldehyde dehydrogenase, perhaps coupled with ABA, that explains why Hamerlynck and coworkers (2002) found ***Syntrichia ruralis*** to be **homoiochlorous** (maintaining constant chlorophyll concentration) in its response to desiccation? Growing in the sun endows these plants with a greater desiccation tolerance than that experienced by shade-grown plants of the same species.

To fit these pieces together requires a great deal of speculation because our knowledge is still too meager. However, let s look at what we know about these pieces and see if we can develop a hypothetical story (Figure 31).

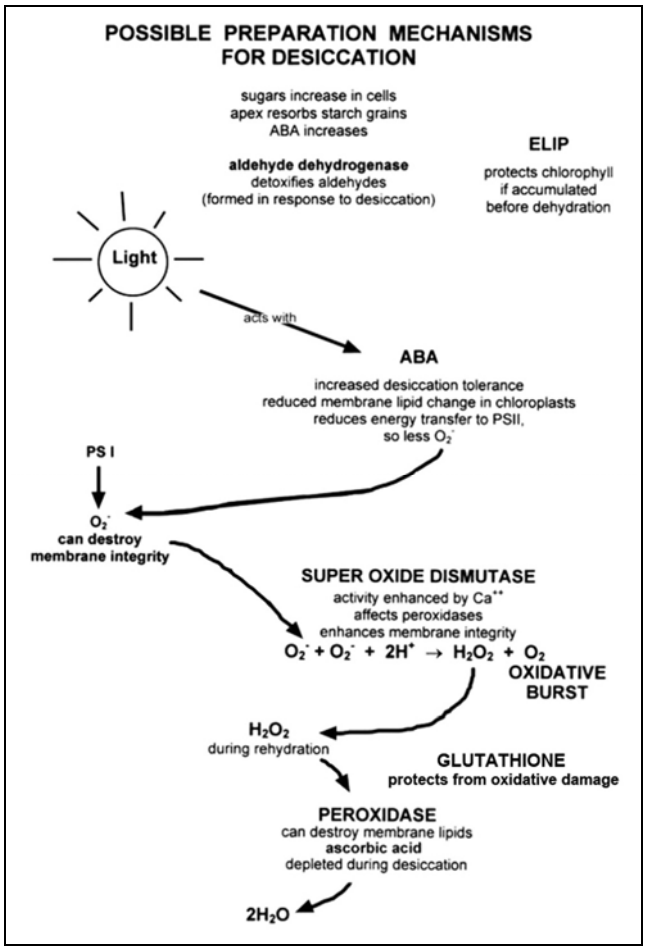

Figure 31. Speculation on possible relationships of the observations that have been made on pre-desiccation events and related rehydration events in desiccation-tolerant bryophytes.

Summary

Membranes become leaky during desiccation. Some mosses protect their membranes with sugars such as stachyose, glucose, erythritol, glycerol, and sucrose.

ABA increases the stress tolerance of bryophytes and is known to turn on the promoters of **stress tolerance genes**. Hence, it is important in controlling transcription. That is consistent with the conclusions of several authors who have determined that drought tolerance in bryophytes evokes control of gene transcription. We also know that **peroxidases** destroy H_2O_2 (**peroxide**), which is harmful to plants. We know that H_2O_2 is responsible for lipid damage of membranes and that lipid peroxidation and increased membrane permeability correlate with the decrease of **superoxide dismutase** (Dhindsa *et al.* 1981). And we know that superoxide dismutase controls **oxygen toxicity** by converting the superoxide radical to less dangerous forms (Michael Potter of Andrew McCammon's group at the University of California, San Diego). Since ***Syntrichia ruralis*** var. ***arenicola*** has a higher concentration of superoxide dismutase than the less desiccation-tolerant ***Dicranella palustris***, we can then hypothesize that the superoxide dismutase is an important contributor to drought tolerance in bryophytes. Perhaps it is one of the 74 proteins produced in response to desiccation stress. Glutathione may help to protect the cells from excessive oxides, but it may have a more important role in protecting against pathogenic microorganisms while they are vulnerable with damaged membranes.

Shoot tips seem able to survive better than other parts of some mosses, but we know nothing about any differences in their biochemistry. New genetic studies are making it possible to learn more about the functions of various compounds in the cells.

Acknowledgments

This chapter, in an early version, has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself.

Literature Cited

Alpert, P. 2000. The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol. 151: 5-17.

Anderson, L. E. 1980. Cytology and reproductive biology of mosses. In: Taylor, R. J. and Leviton, A. E. (eds.). The Mosses of North America. Pacific Division AAAS, San Francisco, pp. 37-76.

Beckett, R. P. 1999. Partial dehydration and ABA induce tolerance to desiccation-induced ion leakage in the moss *Atrichum androgynum*. S. Afr. J. Bot. 65(3): 212-217.

Beckett, R. P. and Hoddinott, N. 1997. Seasonal variations in tolerance to ion leakage following desiccation in the moss *Atrichum androgynum* from a KwaZulu-Natal Afromontane forest. J. S. Afr. Bot. 63(5): 276-279.

Beckett, R. P., Csintalan, Z., and Tuba, Z. 2000. ABA treatment increases both the desiccation tolerance of photosynthesis,

and nonphotochemical quenching in the moss *Atrichum undulatum*. Plant Ecol. 151: 65-71.

Beckett, R. P., Minibayeva, F. V., Lüthje, S., and Böttger, M. 2004. Reactive oxygen species metabolism in desiccation-stressed thalli of the liverwort *Dumortiera hirsuta*. Physiol. Plant. 122: 3-10.

Bewley, J. D. 1979. Physiological aspects of desiccation tolerance. Ann. Rev. Plant Physiol. 30: 195-238.

Bruns, I., Sutter, K., Menge, S., Neumann, D., and Krauss, G. J. 2001. Cadmium lets increase the glutathione pool in bryophytes. J. Plant Physiol. 158: 79-89.

Burch, J. and Wilkinson, T. 2002. Cryopreservation of protonemata of *Ditrichum cornubicum* (Paton) comparing the effectiveness of four cryoprotectant pretreatments. Cryo-letters 23(3): 197-208.

Burritt, D. J. 2008. Glutathione metabolism in bryophytes under abiotic stress. In: Kahn, N. A., Singh, S., and Umar, S. Sulfur Assimilation and Abiotic Stress in Plants. Springer, Berlin, Heidelberg, pp. 303-316.

Carvalho, R. C. de, Catalá, M., Silva, J. M. da, Branquinho, C., and Barreno, E. 2012. The impact of dehydration rate on the production and cellular location of reactive oxygen species in an aquatic moss. Ann. Bot. 110: 1007-1016.

Chen, X., Zeng, Q., and Wood, A. J. 2002. The stress-responsive *Tortula ruralis* gene ALDH21A 1 describes a novel eukaryotic aldehyde dehydrogenase protein family. J. Plant Physiol. 159: 677-684.

Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). Biotropica 24(2a): 121-133.

Cruz de Carvalho, R., Bernades da Silva, A., Soares, R., Almeida, A.M, Coelho, A.V., Marques da Silva, J., and Branquinho, C. 2014. Differential proteomics of dehydration and rehydration in bryophytes: Evidence towards a common desiccation tolerance mechanism. Plant Cell Environ. 37: 1499-1515.

Cruz de Carvalho, R., Bernades da Silva, A., Branquinho, C., and Marques da Silva, J. 2015. Influence of dehydration rate on cell sucrose and water relations parameters in an inducible desiccation tolerant aquatic bryophyte. Environ. Exper. Bot. 120: 18-22.

Cuming, A. C., Cho, S. H., Kamisugi, Y., Graham, H., and Quatrano, R. S. 2007. Microarray analysis of transcriptional responses to abscisic acid and osmotic, salt, and drought stress in the moss, *Physcomitrella patens*. New Phytol. 176: 275-287.

Dhindsa, R. S. 1991. Drought stress, enzymes of glutathione metabolism, oxidation injury, and protein synthesis in *Tortula ruralis*. Plant Physiol. 95: 648-651.

Dhindsa, R. S. and Matowe, W. 1981. Drought tolerance in two mosses: Correlated with enzymatic defence against lipid peroxidation. J. Exper. Bot. 32: 79-91.

Dhindsa, R. S., Plumb-Dhindsa, P., and Thorpe, T. A. 1981. Leaf senescence: Correlated with increased levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide dismutase and catalase. J. Exper. Bot. 32: 93-101.

Duckett, J. G. and Ligrone, R. 2004. There are many ways of making water-conducting cells but what about stomata? Field Bryol. 82: 32-33.

Duckett, J. G. and Renzaglia, K. S. 1988. Ultrastructure and development of plastids in bryophytes. Adv. Bryol. 3: 33-93.

Fisher, K. M. 2008. Bayesian reconstruction of ancestral expression of the LEA gene families reveals propagule-derived desiccation tolerance in resurrection plants. Amer. J. Bot. 95: 506-515.

Gong, M., Chen, S.-N., Song, Y.-Q., and Li, Z.-G. 1997. Effect of calcium and calmodulin on intrinsic heat tolerance in relation to antioxidant systems in maize seedlings. Austral. J. Plant Physiol. 23: 371-379.

Gupta, R. K. 1977. An artefact in studies of the responses of respiration of bryophytes to desiccation. Can. J. Bot. 55: 1195-1200.

Guschina, I. A., Harwood, J. L., Smith, M., and Beckett, R. P. 2002. Abscisic acid modifies the changes in lipids brought about by water stress in the moss *Atrichum androgynum*. New Phytol. 156: 255-264.

Hallet, J. N., Mansour, K. S., and Lecocq, F. M. 1987. Evolution de la structure plastidiale et des reserves polysaccharidiques au cours de la deshydratation des gametophytes feuilles du *Polytrichum formosum* Hedw. (Polytrichales). J. Bryol. 14: 765-777.

Hamerlynck, E. I., Csintalan, Z., Nagy, Z., Tuba, Z., Goodin, D, and Henebry, G. I. 2002. Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss *Tortula ruralis*. Oecologia 131: 498-505.

Hartung, W. 2010. The evolution of abscisic acid (ABA) and ABA function in lower plants, fungi and lichen. Funct. Plant Biol. 37: 806-812.

Hartung, W., Weiler, E. W., and Volk, O. H. 1987. Immunochemical evidence that abscisic acid is produced by several species of Anthocerotae and Marchantiales. Bryologist 90: 393-400.

Hartung, W., Hellwege, E. M., and Volk, O. H. 1994. The function of abscisic acid in bryophytes. J. Hattori Bot. Lab. 76: 59-65.

Hellwege, E. M., Volk, O. H., and Hartung, W. 1992. A physiological role of abscisic acid in the liverwort *Riccia fluitans*. J. Plant Physiol. 140: 553-556.

Hirata, T., Ashida, Y., Mori, H., Yoshinaga, D., and Goad, L. J. 2000. A 37-kDa peroxidase secreted from liverworts in response to chemical stress. Phytochemistry 55: 197-202.

Kranner, I., Beckett, R. P., Wornik, S., Zorn, M., and Pfeifhofer, H. W. 2002. Revival of a resurrection plant correlates with its antioxidant status. Plant J. 31: 13-24.

Kranner, I., Beckett, R., Hochman, A., and Nash, T. H. III. 2008. Desiccation-tolerance in lichens: A review. Bryologist 111: 576-593.

Lehtonen, M. T., Akita, M., Frank, W., Reski, R., and Valkonen, J. P. 2012. Involvement of a class III peroxidase and the mitochondrial protein TSPO in oxidative burst upon treatment of moss plants with a fungal elicitor. Molec. Plant-Microbe Interac. 25: 363-371.

Leinenweber, G., Stegen, S., and Diaz-Palma, P. 2009. Increase of total glutathione as a response to Cd induced stress in a Chilean endemic bryophytes (*Thuidium* sp.). J. Chilean Chem. Soc. 54: 401-404.

Low, P. S. and Merida, J. R. 1996. The oxidative burst in plant defense: function and signal transduction. Physiol. Plant. 96: 533-542.

Mayaba, N., Beckett, R. P., Csintalan, Z., and Tuba, Z. 2001. ABA increases the desiccation tolerance of photosynthesis in the Afromontane understorey moss *Atrichum androgynum*. Ann. Bot. 88: 1093-1100.

Mayaba, N., Minibayeva, F., and Beckett, R. P. 2002. An oxidative burst of hydrogen peroxide during rehydration

following desiccation in the moss *Atrichum androgynum*. New Phytol. 155: 275-283.

Minibayeva, F. and Beckett, R. P. 2001. High rates of extracellular superoxide production in bryophytes and lichens, and an oxidative burst in response to rehydration following desiccation. New Phytol. 152: 333-341.

Minibayeva, F. V., Kolesnikov, O. P., Gordon, L. K. 1998. Contribution of a plasma membrane redox system to the superoxide production by wheat roots. Protoplasma 205: 101-106.

Pence, V. C. 1998. Cryopreservation of bryophytes: the effects of abscisic acid and encapsulation dehydration. Bryologist 101: 278-281.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. International Symposium on Bryophyte Ecology, Edinburgh, UK.

Proctor, M. C., Ligrone, R., and Duckett, J. G. 2007. Desiccation tolerance in the moss *Polytrichum formosum*: Physiological and fine-structural changes during desiccation and recovery. Ann. Bot. 99: 75-93.

Robertson, E. J. 1991. A cytological study of the Musci. Ph.D. Dissertation. University of London.

Robinson, S. A., Wasley, J., Popp, M., and Lovelock, C. E. 2000. Desiccation tolerance of three moss species from continental Antarctica. Austral. J. Plant Physiol. 27: 379-388.

Saxena, A. and Saxena, A. 2012. Bioaccumulation and glutathione-mediated detoxification of copper and cadmium in *Sphagnum squarrosum* Crome Samml. Environ. Monitor. Assess. 184: 4097-4103.

Schwabe, W. W. 1990. Lunularic acid in growth and dormancy of liverworts. In: Chopra, R. N. and Bhatla, S. C. (eds.). Bryophyte Development: Physiology and Biochemistry, CRC Press, Ann Arbor, pp. 245-257.

Seel, W. E., Hendry, G. A. F., and Lee, J. A. 1992a. Effects of desiccation on some activated oxygen processing enzymes and anti-oxidants in mosses. J. Exper. Bot. 43: 1031-1037.

Seel, W. E., Hendry, G. A. F., and Lee, J. A. 1992b. The combined effects of desiccation and irradiance on mosses from xeric and hydric habitats. J. Exper. Bot. 43: 1023-1030.

Shiono, T., Nakata, M., and Satoh, T. 2000. Superoxide dismutases in bryophytes and considerations of their evolution for adaptation to the land environment: A review. Bryol. Res. 7: 317-322

Smirnoff, N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol. 125: 27-58.

Takezawa, D., Komatsu, K., and Sakata, Y. 2011. ABA in bryophytes: how a universal growth regulator in life became a plant hormone? J. Plant Res. 124: 437-453.

Wang, X. Q., Yang, P. F., Liu, Z., Liu, W. Z., Hu, Y., Chen, H., Kuang, T. Y., Pei, Z. M., Shen, S. H., and He, Y. K. 2009. Exploring the mechanism of *Physcomitrella patens* desiccation tolerance through a proteomic strategy. Plant Physiol. 149: 1739-1750.

Werner, O., Ros Espín, R. M., Bopp, M., and Atzorn, R. 1991. Abscisic-acid-induced drought tolerance in *Funaria hygrometrica* Hedw. Planta 186: 99-103.

White, J. F. and Torres, M. S. 2010. Is plant endophyte-mediated defensive mutualism the result of oxidative stress protection? Physiol. Plant.138: 440-446.

CHAPTER 7-8

WATER RELATIONS: HABITATS

TABLE OF CONTENTS

Habitat Relations 7-8-2
Peatlands 7-8-7
Aquatic Habitats 7-8-9
Arid Habitats 7-8-9
    Sporophyte Damage 7-8-15
    Desiccation from Salt 7-8-17
Flood Plains 7-8-17
Arctic and Antarctic 7-8-20
Forest Floor 7-8-22
Temperate Epiphytes 7-8-22
Tropics, Rain Forests, and Cloud forests 7-8-22
    Epiphytes 7-8-26
    Pendent Mosses 7-8-26
    Altitude Differences in the Tropics 7-8-25
Summary 7-8-27
Acknowledgments 7-8-27
Literature Cited 7-8-27

CHAPTER 7-8
WATER RELATIONS: HABITATS

Figure 1. ***Bryum caespiticium*** at a high elevation where winds and ice crystals contribute to desiccation, but where at other times fog can maintain moisture without rain. Photo by Michael Lüth, with permission.

Habitat Relations

Proctor (2014) summarized the importance of water relations for bryophytes in their invasion of land. He pointed out that the poikilohydric strategy is optimal at smaller scales, *i.e.*, bryophytes. Microhabitat and habitat structure are important in conferring the hydration state of bryophytes, and drought sensitivity varies according to species (Irmscher 1912). Norris (1990) found that ***Braunfelsia*** disappeared from some areas of tropical rain forests in Papua New Guinea following disturbance to the forest because of the increased dehydration frequency and the admission of greater wind movement. In the Mediterranean area in the southern and southeastern Iberian Peninsula, Varo and coworkers (1992) found that as the climate has become drier and warmer the bryophyte taxa have changed, with leafy liverworts and pleurocarpous mosses diminishing and ***Sphaerocarpos*** (Figure 2) and acrocarpous mosses becoming more prominent. In central Sweden, greater numbers of bryophytes occur in spruce forests on more moist north-facing slopes, whereas vascular plants are more abundant on the exposed south-facing slopes (Söderström 1981).

Figure 2. ***Sphaerocarpos michelii***, member of a genus that becomes more prominent as the climate dries. Photo by Michael Lüth, with permission.

Bryologists learn inductively through field experience that certain bryophytes are characteristic of dry habitats and others of wet habitats. Actual studies that correlate these conditions with species are less common than descriptive observations, with a number of these being relative to water level in peatlands. Bates *et al*. (2004) used canonical correspondence analysis (CCA) to develop a more rigorous approach to these relationships by sampling epiphytes along a transect across southern Britain from southwest to northeast. With climate, presence of water courses, and forest cover contributing to the analysis, they determined that ***Frullania tamarisci*** (Figure 3), ***Metzgeria temperata*** (Figure 4), ***Microlejeunea ulicina*** (Figure 5), ***Neckera pumila*** (Figure 6), and ***Hypnum andoi*** (Figure 7) were restricted to habitats with high moisture availability. On the other hand, ***Syntrichia ruralis*** (Figure 39), ***Grimmia pulvinata*** (Figure 8), ***Tortula muralis*** (Figure 9), and ***Aulacomnium androgynum*** (Figure 10) only occurred as epiphytes in locations with low moisture. They did not sample these species in other habitats.

Figure 5. ***Microlejeunea ulicina***, a leafy liverwort that is restricted to areas with high moisture levels. Photo by Michael Lüth, with permission.

Figure 3. ***Frullania tamarisci***, a leafy liverwort that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Neckera pumila***, a moss that is restricted to areas of high moisture content. Photo by Jan-Peter Frahm, with permission.

Figure 4. ***Metzgeria temperata***, a leafy liverwort that is restricted to areas of high moisture levels. Photo by Michael Lüth, with permission.

Figure 7. ***Hypnum andoi*** near Swallow Falls in Wales, a moss that is restricted to areas with high moisture content. Photo by Janice Glime.

Figure 8. ***Grimmia pulvinata***, a cushion moss that can only survive as an epiphyte in areas that have high moisture. Photo by Barry Stewart, with permission.

Figure 9. ***Tortula muralis*** habitat on a wall. This moss is unable to live as an epiphyte unless the habitat has low moisture levels. Photo by Janice Glime.

Figure 10. ***Aulacomnium androgynum***, a moss that can only survive as an epiphyte in areas that have high moisture. Photo by Jan-Peter Frahm, with permission.

In mature black spruce forests of central Alaska, the endohydric ***Polytrichum commune*** (Figure 11) is able to avoid moisture stress more so than such ectohydric taxa as ***Hylocomium splendens*** (Figure 12; Skré *et al.* 1983). The latter species remains below its compensation point for water for nearly 50% of the July growing season.

Figure 11. ***Polytrichum commune***, an endohydric moss that is able to avoid moisture stress in black spruce forests more readily than ectohydric taxa. Photo by Michael Lüth, with permission.

Figure 12. ***Hylocomium splendens***, an ectohydric moss. Photo by Janice Glime.

Open expanses of urban areas are notoriously devoid of extensive bryophyte cover, even on trees where taxa are already xerophytically adapted. Hébrard and Rolando (1985) found that when comparing four holm-oak thickets in France, species composition correlated more with plot exposure than with thicket age, suggesting that desiccation, light, and temperature may be most influential. Sheard (1968) likewise found a correlation between the prevailing north wind and the pattern of moss-lichen heath on Jan Mayen Island.

Among the most significant climatic stress inducers for mosses are high temperatures, frost, and drought (Longton 1979). Dry mosses are typically much more heat resistant than wet mosses. For example, Nörr (1974) found that eight European mosses reach lethal limits at 42-51ºC when turgid, but survive to 85-110ºC when dry. Lange (1955) found similar dry survival of mosses from 70-110ºC. Temperature relationships will be discussed more thoroughly in the chapter on temperature.

These relationships also exemplify that, although bryophytes are able to survive on rocky and shallow substrates with little water, they are unable to compete with the tracheophytes in areas where there is sufficient soil, light, and moisture for the tracheophytes to root. But at the extremes, bryophytes may have an advantage. Therefore, it is fitting to conclude our attempt to understand the water stresses of bryophytes by comparing them at the two extremes, the aquatic and the arid habitats.

Using electrolyte leakage as an indication of desiccation stress, Šinžar-Sekulić*et al*. (2005) compared the desiccation tolerance of three mosses from different moisture regimes. ***Thamnobryum alopecurum*** (Figure 13), a moss of open, vertical limestone cliffs, has the highest degree of desiccation tolerance among these three. ***Anomodon viticulosus*** (Figure 14), a moss of limestone rocks in the forest, releases electrolytes under desiccation, causing pronounced changes in the cells. The aquatic moss ***Platyhypnidium riparioides*** (Figure 15) suffers irreversible change following desiccation. It is likely that speed of drying plays a role for the latter species because its frequency on emergent rock habitats suggests that it should be adapted to slow drying. Nevertheless, it seems to live where it stays moist even during periods of low water levels.

Figure 13. ***Thamnobryum alopecurum***, a moss that has high desiccation tolerance on limestone cliffs. Photo by Michael Lüth, with permission.

Figure 14. ***Anomodon viticulosus***, a moss of limestone rocks that releases electrolytes when desiccated. Photo by Michael Lüth, with permission.

Among the hornworts (**Anthocerotophyta**) little information exists on desiccation tolerance. Some are drought avoiders, producing special structures that survive periods of desiccation (Vitt *et al*. 2014). These, occurring on hornworts of seasonally dry localities, include abundant swollen, marginal or apical tubers on the thalli (***Phaeoceros*** spp.; Figure 16-Figure 17) or long-stalked, subterranean ventral tubers (***Phymatoceros***; Figure 18). Both of these special tubers form as the sporophytes mature and persist in the soil crust or soil bank after the vegetative thallus has deteriorated. Rainfall causes these tubers to germinate and form new plants (Crandall-Stotler *et al*. 2006). Hartung *et al*. (1994) found that these tubers contain large amounts of ABA, a hormone known to induce desiccation tolerance in bryophytes (Pence *et al*. 2005). These tubers can survive at least nine months of dryness and still germinate (Vitt *et al*. 2014).

Figure 15. ***Platyhypnidium riparioides***, an aquatic moss that can suffer irreversible damage from desiccation. Photo by Des Callaghan, with permission.

Figure 16. ***Phaeoceros*** sp. showing abundance of light green tubers in the center of the thallus. Photo by Juan Larrain, with permission.

Figure 17. ***Phaeoceros pearsonii*** with thickened tubers. Photo by Li Zhang, with permission.

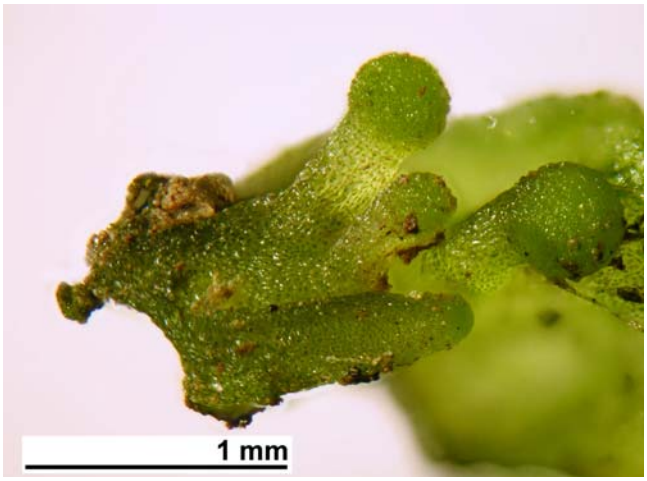

Figure 18. ***Phymatoceros bulbosus*** ventral side with tubers. Photo by David Wagner, with permission.

Other hornworts take advantage of short life cycles. For example, rapid spore release in ***Notothylas*** (Figure 19), coupled with the ability to survive many years dry (Renzaglia *et al*. 2009) permit this genus to avoid drought conditions.

Figure 19. ***Notothylas orbicularis*** showing numerous young horizontal sporophytes. Photo by Michael Lüth, with permission.

Liverworts are known for loving damp habitats, but they contain their xerophytic members as well. Seppelt (pers. comm. 1999) relayed to me that these include species surviving in as little as 150 mm of rainfall per year [***Fossombronia*** (Figure 20), ***Asterella*** (Figure 21), ***Plagiochasma*** (Figure 22)]. At somewhat higher levels (200 mm), such taxa as ***Lethocolea*** (Figure 23), ***Cephaloziella*** (Figure 24), ***Riella*** (Figure 66), ***Enigmella***, and ***Gongylanthus*** (Figure 25) appear. ***Enigmella*** is ephemeral in its vegetative phase, but its reproductive structures are well suited to their environment. Some taxa survive drought by having a shortened life cycle, *e.g.* ***Riccia cavernosa*** in the Arctic (Seppelt & Laursen 1999).

Figure 20. ***Fossombronia angulosa*** with capsule, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Des Callaghan, with permission.

Figure 21. ***Asterella lindenbergiana*** with archegoniophores, a member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Martin Hutten, with permission.

Figure 22. ***Plagiochasma appendiculatum***, member of a genus in which some species survive in as little as 150 mm annual rainfall. Photo by Michael Lüth, with permission.

Figure 23. ***Lethocolea glossophylla***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Cephaloziella*** cf ***hampeana***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Barry Stewart, with permission.

Figure 25. ***Gongylanthus ericetorum***, member of a genus in which some species survive in 200 mm annual rainfall. Photo by Michael Lüth, with permission.

Peatlands

Peatlands provide a good ecosystem for comparing adaptations for differences in moisture regimes by habitat. But the dominant moss, ***Sphagnum***, has unusual structural adaptations that can complicate this analysis.

Wagner and Titus (1984) compared desiccation tolerance of the hummock species ***Sphagnum nemoreum*** (Figure 26) to that of the hollow species ***S. fallax*** (Figure 27). The hollow species is more desiccation tolerant than the hummock species. It has both a higher number of plants surviving and a better recovery of its photosynthetic rate. However, its ability to recover decreases as the desiccation periods are lengthened or the water content is decreased. Despite being close to the water, ***S. fallax*** apparently dries more frequently and for longer periods of time than does ***S. nemoreum***. The latter species, instead, is able to remain moist in the field by holding more water when the habitat dries.

Figure 26. ***Sphagnum nemoreum***, a compact hummock moss. Photo by Michael Lüth, with permission.

Figure 27. ***Sphagnum fallax***, a loose moss of hollows. Photo by David Holyoak, with permission.

Schipperges and Rydin (1998) compared the responses of photosynthetic CO_2 exchange in five species of ***Sphagnum*** in response to tissue water content. These species ranged in microhabitat from hummock top (***S. fuscum***; Figure 28), hummock mid to top [***S. papillosum*** (Figure 29) & ***S. magellanicum*** (Figure 30)], wet areas of ombrotrophic bogs and ditches (***S. balticum***; Figure 31), to submerged (***S. cuspidatum***; Figure 32). Laboratory experiments using infrared gas analysis (IRGA) measured recovery of net photosynthesis after several long-lasting desiccation/rehydration events. One important structural adaptation that emerged is the importance of contact between capitula and basal parts of the mosses; if the

capitula were isolated from the water table, they were unable to recover from complete desiccation (<10-20% of compensation point water content; 15°C for 2-4 days). It is interesting that they found no relationship between recovery of net photosynthesis and wetness of the natural habitat. Rather, those species that live under regularly drying conditions are able to avoid death by themselves avoiding drying out, using high capillarity or a dense growth form such as that of ***S. fuscum*** (Figure 28).

Figure 28. ***Sphagnum fuscum***, a hummock top species. Photo by Michael Lüth, with permission.

Figure 29. ***Sphagnum papillosum***, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.

Figure 30. ***Sphagnum magellanicum***, a species of mid to top of hummocks. Photo by Michael Lüth, with permission.

Figure 31. ***Sphagnum balticum***, a species of wet areas of bogs and ditches. Photo by Michael Lüth, with permission.

Figure 32. ***Sphagnum cuspidatum***, a submerged species. Photo by Jan-Peter Frahm, with permission.

Hájek and Vicherová (2013) concluded that ***Sphagnum*** species have inducible desiccation tolerance. These species are generally desiccation intolerant, instead using mechanisms to avoid internal desiccation, as noted by Schipperges and Rydin (1998). Hájek and Vicherová tested the inducible nature of their tolerance by using various bryophyte species, including ***Sphagnum***. They hardened the bryophytes by slow drying, ABA application, and chilling or frost. Both chilling and frost can create desiccating conditions by drawing water from the cells through the hygroscopic nature of ice crystals, much like the effects of freezer burn in your freezer. Presuming that the tolerance was inducible, they monitored the seasonal changes in desiccation tolerance of bog bryophytes. Among these, ***Sphagnum*** species in hollows and lawns developed desiccation tolerance several times during the year as a response to reduced precipitation and lowered water table. The hummock and aquatic species developed this tolerance only in the autumn, possibly responding to frost. Following initial de-hardening in the lab, untreated ***Sphagnum*** shoots lacked desiccation tolerance. On the other hand, all hardening treatments except chilling induced desiccation tolerance in all groups except those in section ***Cuspidata*** (Figure 32), a submersed species. They suggest that lack of adequate desiccation tolerance may prevent ***Sphagnum*** establishment in the drier habitats that are otherwise suitable. Those species that avoid desiccation typically do so by forming compact hummocks – or living submersed. Thus, hummock species invest their

resources in water retention, avoiding desiccation, but have a lower ability to develop desiccation tolerance.

Peatlands typically have moisture gradients, and Hettenbergerova *et al*. (2013) took advantage of this gradient to compare species richness relative to water availability. They were fortunate to have a system that graded from a spring fen to a semi-dry grassland in the Czech and Slovak Republics. They found that the number of species of tracheophytes tended to increase toward the lower moisture values. The species richness had a negative correlation with the N:P biomass ratio, whereas the percentage of endangered species had a positive correlation. These relationships for bryophytes differed markedly from those of the tracheophytes. Instead, bryophyte species richness decreased linearly toward the dry end of the transects, and there was no correlation with any of the nutrient measurements (N, P, K, C, Ca). Furthermore, the bryophytes exhibited a very high percentage of specialists in fen plots.

Sagot and Rochefort (1996) were concerned about the effects of desiccation on regeneration. They found that fragments of ***Sphagnum fallax*** (Figure 27), ***S. fuscum*** (Figure 28), and ***S. magellanicum*** (Figure 30) could survive 14 days without water when air dried at 20°C, relative humidity ~60%, but regeneration was delayed. ***Sphagnum fallax*** and ***S. magellanicum*** survived better than did ***S. fuscum***.

Aquatic Habitats

The aquatic bryophytes are distributed worldwide, but they seem to be more common in temperate than in tropical areas. Aquatic species are classified as **obligate aquatics**, having little or no tolerance to drought conditions, **facultative aquatics**, having some degree of tolerance to desiccation and xerophytic conditions, and **semi-aquatic emergents** (Vitt & Glime 1984), being in locations where they are partly in the water and partly out of it, but usually moist (Figure 33).

Figure 33. ***Fontinalis novae-angliae*** submerged and ***Plagiochila porelloides*** on the rock above the water in a New Hampshire stream. The ***P. porelloides*** is subject to intermittent flooding but can become dry when the stream level is low in mid and late summer. Photo by Janice Glime.

Rehydration in aquatic mosses is much like that of tracheophytes. Whereas many mosses are able to protect their ribosomes during dehydration (Bewley 1974), permitting rapid recovery of protein synthesis and respiration upon rehydration, aquatic bryophytes are not. Instead, irreversible ribosome damage occurs (Krupa 1977). For example, ***Cratoneuron*** (Figure 34), a semi-aquatic moss, loses ATP during rapid drying, and with its damaged ribosomes it is unable to replace it upon rehydration (Bewley & Gwozdz 1975). Aquatic mosses typically suffer membrane damage during desiccation, but **xeric** (dry habitat) mosses often do not (Brown & Buck 1979). Thus, in aquatic mosses, rehydration results in loss of nutrients.

Figure 34. ***Cratoneuron filicinum***, a moss known to lose ATP during rapid drying. Photo by Ivanov, with permission.

Even such obligate aquatic mosses as ***Fontinalis*** are subject to periods low water when they are exposed above water. Carvalho *et al*. (2011) found that the aquatic moss ***Fontinalis antipyretica*** (Figure 65) demonstrates desiccation tolerance. Laboratory experiments can be misleading because this species requires slow drying in order to survive, supporting the hypothesis of induced desiccation tolerance. In fact, Cruz de Carvalho *et al*. (2011) concluded that the protein profiles following rehydration were similar to those of the terrestrial mosses ***Physcomitrella patens*** and ***Syntrichia ruralis*** (Figure 39). They concluded that desiccation tolerance mechanisms were similar regardless of habitat.

Arid Habitats

Contrary to the popular concept that mosses must grow in wet places, a number of species are **xerophytic**, that is, adapted to places like the dry, hot desert. In such habitats, some mosses are able to absorb water from dew and night air, permitting brief photosynthesis during the early hours of morning. They dry again each day, cycling on a 24-hour wet-dry cycle (Kappen *et al*. 1979). Where the sun reaches the mosses directly, as on the south-facing slopes in North American deserts, the temperature can increase by as much as 20ºC in the first 30 minutes of daylight, thus providing too short a period for the moss to gain photosynthetic energy before drying out (Nash *et al*. 1977). In such locations the mosses are restricted to the north-facing slopes. The biomass is quite small, less than 2 g m^{-2}, but at least 18 different species are able to survive, the most common being tuft-forming taxa such as ***Syntrichia ruralis*** (Figure 39), ***Grimmia laevigata*** (Figure 36), and ***Bryum caespiticium*** (Figure 1).

One advantage of having sufficient moisture in the desert habitat is that it can provide evaporative cooling. But that does not seem to be the case in all situations. In the Mojave Desert, Nevada, USA, ***Crossidium***

crossinervium (Figure 62) experienced temperatures above ambient, independent of the state of hydration (Stark 2005). During cooler months, the moss patch exhibited a temperature lower than ambient, again with state of hydration failing to play a role. The periods of hydration were essentially restricted to the cooler months of October to April with hydration lasting 3.7-4.9 days. The longest dry period was 191 days during the measurement period. In late winter, drying was slow, lasting several days, but in the summer the mosses were dry in as little as three hours.

Peatland bryophytes are not the only ones that practice avoidance and tolerance. These practices are also common among bryophytes that live in some of the most harsh moisture conditions on the planet. One mechanism is to go dormant during the dry periods, surviving as spores, gemmae, and probably in some cases protonemata (Vitt *et al*. 2014). Such an **escape strategy** is advantageous to bryophytes that lack a physiological tolerance to desiccation in the leafy gametophore (Figure 35). Liverworts have fewer genera with an escape strategy, but many thallose liverworts have tubers or other means, especially ***Riccia***, to survive (see Figure 69); many leafy liverworts have gemmae.

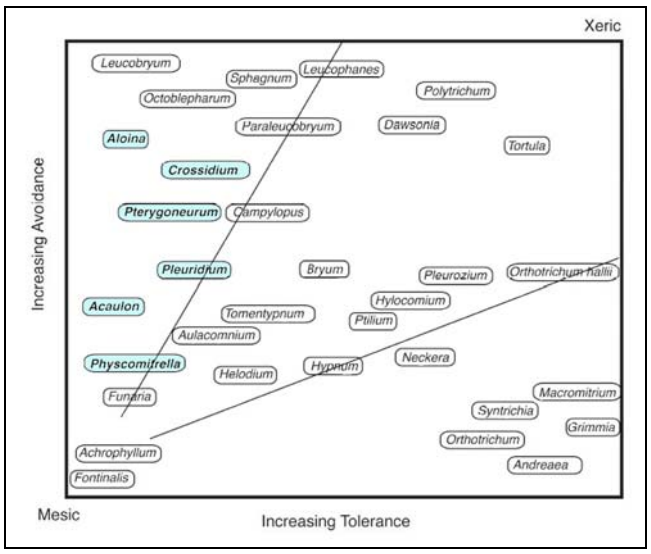

Figure 35. Comparison of representative moss genera that are able to use desiccation avoidance compared to desiccation tolerance. Those genera in blue frames are able to use escape strategies. Modified from Vitt *et al*. 2014.

Figure 36. ***Grimmia laevigata***, a desert survivor. Photo by Michael Lüth, with permission.

In the Sonoran Desert of North America, Alpert (1979) found that an overnight storm provided 85% of the saturated water contents, available at 6 a.m., for ***Bryum capillare*** (Figure 37), ***Grimmia*** spp. (Figure 36), ***Syntrichia*** spp. (Figure 39), and ***Weissia controversa*** (Figure 38). By 9 a.m., eleven of the twelve species investigated had only 2 g water per g of plant dry mass, and by 3 p.m., only 0.5 g remained. By 5 p.m., less than 0.1 g per gram of plant remained, resulting in only about 9 hours of water available from that rare storm. Richardson (1981) points out that it is not damage by drought that eliminates many species from the desert, but the very short time available for photosynthesis.

Figure 37. ***Bryum capillare*** on a tombstone, a moss that benefits from short moisture episodes, but that holds water for only about 9 hours after a desert storm. Photo by Andrew Fogg, through Creative Commons.

Figure 38. ***Weissia controversa*** dry, a moss that may have only 9 hours of hydration following a desert storm. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

One adaptation that permits some mosses to tolerate frequent dehydration/rehydration cycles is that those xeric mosses with undamaged membranes are able to retain ions by binding them to the cell wall (Brown & Buck 1979). Another adaptation in the desert moss is that rapid water loss, typical of the desert, can result in a retention of 50% of the polysomes, whereas slow drying can completely deplete them. Fortunately, in drought-tolerant mosses like ***Syntrichia ruralis*** (Figure 39), the polysomes can be strongly rebuilt after two hours of rehydration (Oliver & Bewley 1984b), but the process continues for a longer

period of time in those that were dried rapidly. RNA synthesis likewise requires six hours after rapid drying and only two hours after slow drying to reach the level of that in non-dried control mosses (Oliver & Bewley 1984a).

Figure 39. ***Syntrichia ruralis***, a drought-tolerant moss. Photo by Michael Lüth, with permission.

One unclear factor in this story is the role of nitrite. Nitrite accumulates during slow dehydration of ***Syntrichia ruralis*** (Figure 39), but not when desiccation is rapid (Mahan *et al.* 1998). Upon rehydration, the nitrite in the slowly-dried moss declines and reaches normal levels within one hour. Mahan and coworkers considered that the nitrite might provide a nitrogen source for the nitrogen metabolism needed during rehydration. On the other hand, Brown and Mahmood (1996) determined that nitrite apparently causes considerable membrane damage in the mesophytic ***Mnium hornum*** (Figure 40); thus we need further research to understand the conditions under which it is detrimental vs adaptive.

Figure 40. ***Mnium hornum***, a moss in which cell membranes suffer damage from elevated nitrite concentrations during dehydration. Photo by David T. Holyoak, with permission.

Marschall (1998) examined the activity of nitrate reductase during desiccation and rehydration of nine bryophytes and concluded that there was no difference in the proportional decrease in nitrogen reductase activity between desiccation-tolerant and non-tolerant bryophyte taxa. Eight of these bryophytes did exhibit detectable nitrate reductase (NR) activity. Pretreatment with KNO_3 did affect the increase in NR activity between these two types, with the desiccation-tolerant ***Syntrichia ruralis*** var. ***arenicola*** (Figure 39) increasing activity by a factor of 3 while the desiccation-intolerant ***Dicranum majus*** (Figure 41) and ***Hookeria lucens*** (Figure 42) had a 6-fold increase in nitrate reductase activity. Following rehydration, ***Syntrichia ruralis*** (Figure 39) exhibited a marked decline in NR activity during the first hour, whereas the epiphytic/saxicolous ***Porella platyphylla*** (Figure 43) maintained a relatively constant low level in the light but increasing NR activity in the dark. While we might assume that these physiological differences relate to survival, it is too early to explain just how this is accomplished.

Proctor (1982) considers such structures as papillae to be adaptive in ensuring that the moss does not spend a long period of time in a semi-dry state, during which it is likely to lose more carbon by respiration than it gains by photosynthesis. He notes that the papilla systems, so common on xerophytic leaves, are often separated by regions where the capillary continuity is broken at high water potentials, causing the leaf to have either an abundant water supply, or none. Such discontinuities could be amplified if the leaf rolls as it dries and bends away from the discontinuity. Vanderpoorten and Engels (2002) considered papillae so important as to be one of only four life history traits contributing to predictability of species occurrence in a particular environment on a regional scale. Nevertheless, experiments on the role of papillae in conserving water have mostly failed (Frey & Kürschner 1991).

Figure 41. ***Dicranum majus*** near Swallow Falls, Wales, a moss that is desiccation-intolerant. Photo by Janice Glime.

Figure 42. ***Hookeria lucens***, a desiccation-intolerant species. Photo by David T. Holyoak, with permission.

Figure 43. ***Porella platyphylla***, an epiphytic/saxicolous liverwort. Photo by Michael Lüth, with permission.

Few bryophytes approach the succulent or sclerophyll strategies known in tracheophytes (Grime 1977), although one might argue for succulence in the Marchantiales. Plants with numerous or large papillae take on the appearance of sclerophylls, and for many years we assumed that papillae functioned to prevent the loss of water. However, as Frey and Kürschner (1991) pointed out, tests to validate that theory have failed. Nevertheless, while it appears that the papillose mosses do not slow down water loss, the papillae may have a function in water uptake (Crandall-Stotler & Bozzola 1991). As discussed earlier with leaf strategies (see Chapter 7-4a of this volume), papillae in ***Andreaeobryum macrosporum*** (Figure 44) are constructed in such a way that they provide a channel for the uptake of water.

Figure 44. ***Andreaeobryum macrosporum***, a moss with papillae that provide a pathway for uptake of water. Botany website, University of British Columbia, Canada, with permission.

I have suggested that papillae on some mosses might also function to scatter light during dry periods, thus aiding in the protection of the chlorophyll from the UV light during the lengthy time the leaf is exposed, with no chance for repair between rainfall events.

Alpert (1979, 1982, 1985, 1988) investigated five species of **poikilohydric** mosses (those that depend on external conditions to regulate their water content): ***Schistidium apocarpum*** (Figure 45), ***Grimmia laevigata*** (Figure 36), ***Hedwigia ciliata*** (Figure 46), ***Orthotrichum rupestre*** (Figure 47), and ***Syntrichia ruralis*** var. ***crinata*** (see Figure 39). These bryophytes are characterized by short cushions of tufted growth, except for ***Hedwigia ciliata***. The latter moss has a whitened appearance due to numerous papillae, and its leaves are closely appressed to the stem when dry. When wet, the leaves spread broadly, causing it to look sufficiently different from its dry state that it causes many bryologists to stop and puzzle over its identity.

Alpert (1979, 1982, 1985, 1988) found that these five mosses were able to colonize unoccupied, stressful boulder habitats, but that they were intolerant of competition or of disturbance beyond their normal desiccation regime. They grew in particular microclimatic niches on the rock substrata and were unable to occupy the most xeric conditions within the same macroclimate, although laboratory studies indicated that they can tolerate both temperatures and droughts that exceed those of the habitats they occupy. Alpert showed through transplant experiments that they could indeed occupy additional locations, suggesting that dispersal and establishment impose limits on their distribution.

Figure 45. ***Schistidium apocarpum*** with capsules, an ectohydric moss. Photo by Michael Lüth, with permission.

Figure 46. ***Hedwigia ciliata***, an ectohydric moss shown here on rock. Photo by Janice Glime.

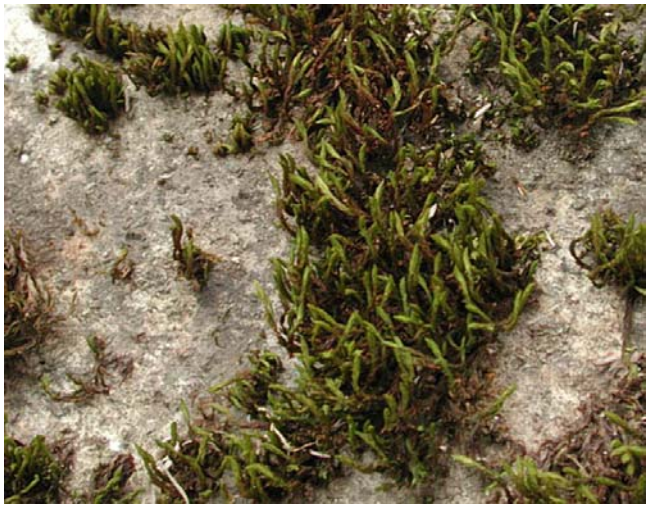

Figure 47. ***Orthotrichum rupestre***, a xerophytic moss on rock. Photo by Michael Lüth, with permission.

The aspect and angle of slope had strong influences on the evaporation stress experienced by these mosses (Alpert 1979, 1982, 1985, 1988). Mosses growing under rock overhangs should experience the least water stress by late day, but do not regain as much moisture as those at 15° and 75° slopes (Figure 48). As expected, mosses at the tops of boulders had the greatest peaks of evaporation stress. Alpert's work illustrates the importance of 24-hour measurements in comparing potential evaporative stresses of different microsites.

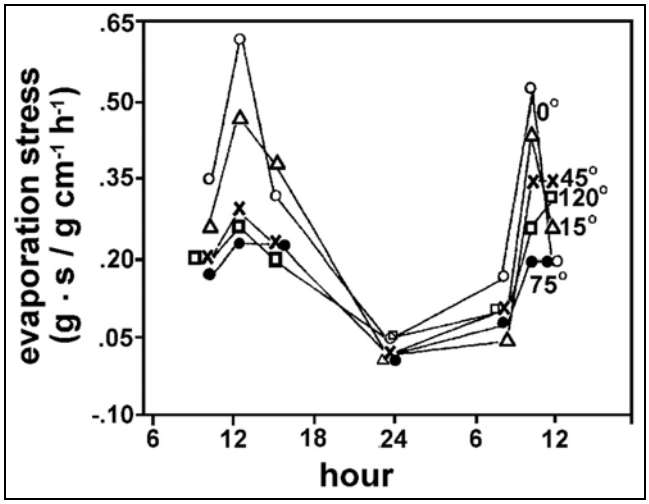

Figure 48. Effects of degree of slope on potential evaporation on 21-22 February 1980 for mosses (based on uniform paper samples) on arid north sides of rocks in five slope microsites. (n=4) Modified from Alpert (1982).

Aspect separated the evaporation stresses even more clearly (Figure 49), with evaporation stress on the east side peaking at about 10:00 hours and at most other aspects peaking at about 12:00 hours (Alpert 1982). Stress on the west side peaked last, at 14:00 hours, but with a lower peak than at the other aspects. The north, as might be expected, had the least daily variation. Although daily evaporation potential was high, a brief nighttime rainfall of no more than 5 mm was sufficient to rewet the moss for several days (Figure 50, Alpert 1982).

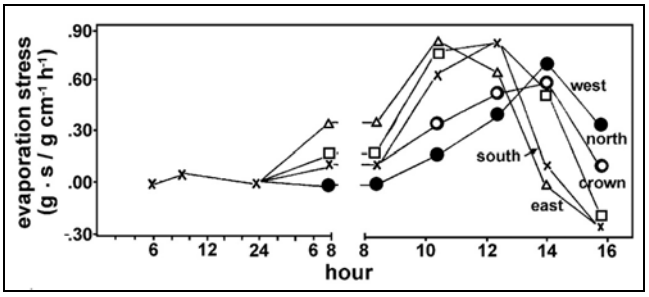

Figure 49. Effect of aspect on potential evaporation on 7-8 March 1980 for mosses (based on uniform paper samples) on arid 45° slope in five aspect microsites. (n=4) Modified from Alpert (1982).

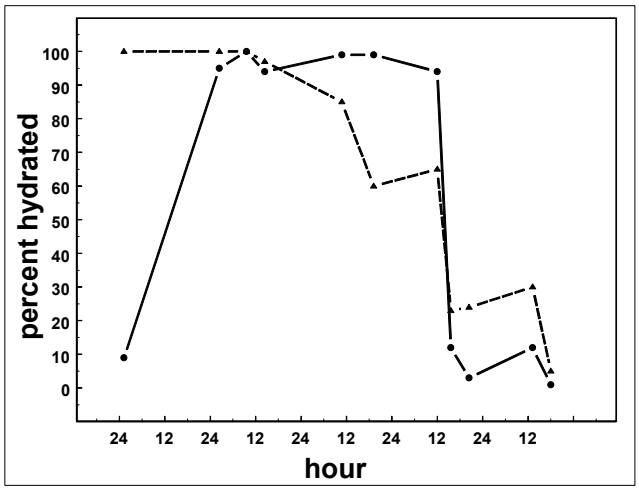

Figure 50. Percent hydration of natural moss cover on boulders following nighttime rainfalls of ~5 mm in spring and winter. Redrawn from Alpert (1982).

Open, exposed soils in temperate climates are arid for bryophytes because of their insignificant soil penetration by which to obtain water. In these habitats, the mosses ***Barbula*** (Figure 51), ***Syntrichia*** (Figure 39), and the thallose liverwort ***Riccia*** (Figure 52) are able to survive (Schofield 1985). The two mosses are both papillose and able to roll their leaves and contort them as they dry. The ***Riccia*** thallus usually has inrolled margins and a thick cuticle; Frey and Kürschner (1991) have demonstrated that thallus and leaf inrolling correlate with increasing aridity, suggesting a protective role. ***Ceratodon*** (Figure 53), ***Funaria*** (Figure 54), and ***Cephaloziella*** (Figure 55) seem to lack any structural adaptations to their sometimes dry habitats, although ***Ceratodon*** does have crispate leaves and rolled margins.

In cryptogamic crusts of arid regions, bryophytes are important in holding water, retaining several times their volume after rainfall (Mücher *et al*. 1988; Rivera-Aquilar *et al*. 2005). This leads to higher germination rates of seed plants compared to areas with no crust (Mücher *et al*. 1988; Rivera-Aquilar *et al*. 2005; Serpe *et al*. 2006)

Figure 51. ***Barbula convoluta*** var. ***commutata***, an ectohydric moss growing on rock over little or no soil. Michael Lüth, with permission.

Figure 52. ***Riccia nigrella***, a thallose liverwort surviving on dry soil. Photo by Michael Lüth, with permission.

Figure 53. ***Ceratodon purpureus*** on rocky soil, a moss that has few structural adaptations to such a dry habitat. Photo by Janice Glime.

A comparison of mosses from a variety of habitats in Israel revealed varying degrees of drought tolerance that related well to their habitats (Di Nola *et al*. 1983). The desert mosses ***Tortula brevissima*** (Figure 56) and ***Trichostomopsis aaronis*** exhibited rapid return of metabolic activity after prolonged drying and were able to resume photosynthesis without new chlorophyll synthesis. The Mediterranean moss ***Barbula fallax*** (Figure 57) behaved similarly to the desert mosses, but ***Homalothecium aureum*** (Figure 58) and ***Didymodon tophaceus*** (Figure 59), more mesic mosses, had slow recovery after desiccation. ***Mniobryum*** sp. (Figure 60) had almost no drought tolerance and was killed by the prolonged drying.

Figure 54. ***Funaria hygrometrica***, a moss with no noticeable xerophytic adaptations, living on sand and rocks. Photo by Michael Lüth, with permission.

Figure 55. ***Cephaloziella stellulifera***, a leafy liverwort that seems to lack structural adaptations to this rock habitat. Photo by David T. Holyoak, with permission.

Figure 56. ***Tortula brevissima***, a desert moss that rapidly returns its metabolic activity upon rehydration. Photo by Michael Lüth, with permission.

Figure 57. ***Barbula fallax***, a Mediterranean moss that resumes metabolic activity rapidly upon rehydration. Photo by Jan-Peter Frahm, with permission.

Figure 58. ***Homalothecium aureum***, a mesic moss. Photo by Michael Lüth, with permission.

Figure 59. ***Didymodon tophaceus***, a mesic moss. Photo by Michael Lüth, with permission.

Longton (1988b) pointed out the importance of dispersal among desert bryophytes, since many of them are drought avoiders. Since sexual reproduction will occur infrequently, he contends that desert mosses should be acrocarpous **perennial stayers** with long-lived, desiccation-tolerant gametophytes, small spores, and long setae. The **annual** taxa are **ephemeral** (short-lived) mosses and liverworts that can develop rapidly after a rain because their dormancy is accomplished by large spores; their capsules are often immersed, presumably shortening the time required to mature and preserving moisture. The **perennial shuttle** species are mostly thallose liverworts that have both desiccation-tolerant gametophytes and large spores. **Fugitives** generally stay only one to two years while the habitat remains suitable at a site and produce small spores that permit them to be dispersed easily.

Figure 60. ***Mniobryum wahlenbergii***, a moss that has little or no drought tolerance. Photo by Jan-Peter Frahm, with permission.

The short duration of the life cycle is one of the advantages provided to many desert bryophytes. In the southwestern desert habitat (USA), the desiccation-tolerant ***Syntrichia ruralis*** (Figure 39) requires a year to reach maturity, producing new innovations in midwinter and growing slowly through spring (Mishler & Oliver 1991). In late summer, it lengthens rapidly, completing its growth by midwinter. Female gametangia are initiated in midwinter and terminate the growth of these innovations. However, the female gametangia are present during the next 6 to 9 months on these innovations, ultimately disappearing some time between June and August. In the New Mexico populations observed by Mishler and Oliver, there were no male gametangia, and thus no sporophytes produced. Consequently, this plant must propagate entirely by vegetative means.

In the Negev Desert, southern Israel, the dioicous moss ***Bryum dunense*** takes advantage of fog and dew prior to the first winter rain to initiate its reproductive organs (Herrnstadt & Kidron 2005). The sporophytes are most common in partially shaded habitats and appear following the winter rains. This reproduction is supplemented by the typically more reliable reproduction through bulbils in the partially shaded and exposed habitats, whereas secondary protonemata are most abundant in the shaded habitats.

Alpert and Oechel (1985) hypothesized that even the xerophytic mosses cannot live in the most xeric habitats due to their inability to maintain a positive carbon balance. ***Grimmia laevigata*** lives under the xeric conditions of rocks and boulders. When subjected to such extreme conditions of long, severe drought and extreme temperatures, this moss supported the hypothesis.

Sporophyte Damage

The leafy gametophyte is not the only generation affected by desiccation. For desert mosses, too little rainfall in early sporophyte development can also be a problem. In the Mojave Desert, Nevada, USA, the moss ***Syntrichia inermis*** (Figure 61) experienced 66% abortion of sporophytes due to a reduced winter-spring rainfall

(Stark 2002). But unusually heavy rains in the summer likewise resulted in an increase in sporophyte abortion from 9 to 43%. Stark suggested that the summer abortions may have been the result of membrane damage resulting from rapid drying as well as from high temperatures while hydrated. ***Crossidium crassinervium*** (Figure 62) experienced similar sporophyte abortions in the same desert (Stark 2005).

Figure 61. ***Syntrichia inermis*** dry, a moss whose sporophytes experience considerable abortion due to desiccation. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 62. ***Crossidium crassinervium*** with one young sporophyte, a moss whose sporophytes experience considerable abortion due to desiccation. Photo by Michael Lüth, with permission.

Grimmia orbicularis (Figure 63) can suffer sporophyte abortion as a result of poor timing. It was summer rainstorms in the Mojave Desert that led to the demise of ~50% of the sporophytes, mostly in the seta elongation phase (Stark 2001). As in ***Syntrichia inermis*** (Figure 61), Stark suggests that the abortion resulted from stresses caused by wet-dry cycles during summer heat, a time when the moss would normally be dry and have arrested metabolism. This may have been complicated by the premature seta elongation that resulted in more exposure during the remainder of the summer or that set in motion the physiology for capsule maturation at a time when insufficient nutrients were available.

The arid and semi-arid lands occupy approximately 40% of the land on planet Earth (Reed *et al*. 2012). Climate change that changes annual rainfall could result in profound mortality of bryophytes growing there. An increase of rainfall frequency, resulting in only a 1.2 mm increase in summer rainfall, reduced the moss cover of ***Syntrichia caninervis*** (Figure 64) from approximately 25% cover to less than 2% in just one growing season. The addition of small precipitation events resulted in a negative carbon balance; larger events are able to maintain carbon balance. The loss of moss cover changed the nitrogen cycling, reducing soil fertility. On the other hand, increased temperature had no effect.

Figure 63. ***Grimmia orbicularis***, a moss that suffers sporophyte abortion if the wet/dry cycles have the wrong timing during sporophyte development. Photo by Michael Lüth, with permission.

Figure 64. ***Syntrichia caninervis***, a desert moss. Photo by Michael Lüth, with permission.

Syntrichia caninervis has served as a model for successful desert living by bryophytes. Wu *et al*. (2015) demonstrated that when only 2 mm of precipitation wets the leaves of ***Syntrichia caninervis*** (Figure 64), the moss loses carbon. It requires 5 mm of precipitation for a carbon gain. Hence, short storms can be detrimental to the moss, explaining the loss of moss cover with the increase in frequency of rainfall and gain of 1.2 mm rain in the Colorado Plateau, USA (Reed *et al*. 2012).

This loss of carbon is despite the rapid recovery of ***Syntrichia caninervis*** (Figure 64). Within only one minute, it recovers 90% of its photosynthetic yield (Zhang *et al*. 2011). In fact, this species can use moisture from dew and fog, collected and directed into the leaf by its hair points (Tao & Zhang 2012). In addition to the collection effect of the hair tips, mosses from dry habitats have high osmotic values that enable them to absorb water vapor from the air. These attributes seem almost contradictory to the

loss of cover due to a minor increase in rainfall events in the desert, but a short daytime rainfall is quite different from the prolonged moisture available from fog or dew at night. Daytime moisture from a short rainfall lasts for a very short time, apparently insufficient to recover the lost energy before high temperatures and evaporation shut it down. Yet this leaves the question of rebuilding energy at night. It suggests that it is the cellular changes that use up one readily available form of energy but do not permit rebuilding it, whereas the hydrated cells from dew are fully functional and ready for photosynthesis with the first light of day – there should be no delay at all. At this time the moss is still cool from the night and evaporation should be slower.

Desiccation from Salt

Salt pans and regions of salt spray, when not under water, can be the most arid conditions of all. Few bryophytes are adapted to this regime, although some species of ***Fontinalis*** (Figure 65) can tolerate **brackish** (somewhat salty, often from a mix of fresh and salt water) waters. The liverworts ***Riella helicophylla*** (Figure 66), ***R. numidica***, and ***Carrpos*** (?) are among the few (Schofield 1985).

Figure 65. ***Fontinalis antipyretica***, member of a genus where some species tolerate brackish water. Photo by Bernd Haynold, through Wikimedia Commons.

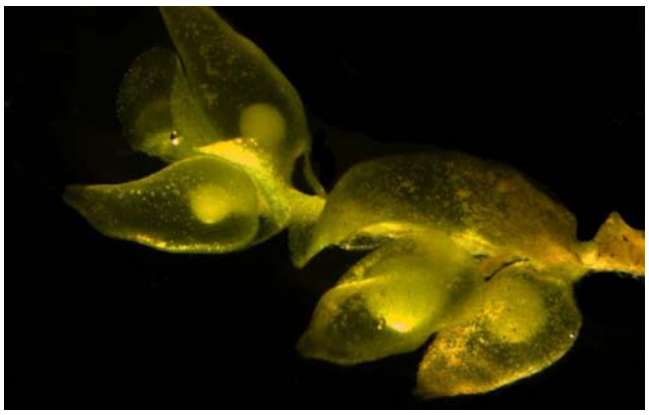

Figure 66. ***Riella helicophylla***, a thallose liverwort that is able to tolerate brackish water. Photo by NACICCA, through Creative Commons.

Flood Plains

The flood plain habitat is one of extremes. For part of the year the inhabitants are under water, but once the water recedes the habitat can become extremely dry. This regime requires different adaptations from other kinds of dry habitats.

A number of thallose liverworts exhibit drought or desiccation tolerance (Figure 69) and are able to live in these alternating habitats (Bischler 1998; Wood 2007). Such genera include fairly small liverworts with thick thalli and short life cycles: ***Corsinia*** (Figure 67), ***Cronisia***, ***Exormotheca*** (Figure 68), ***Monocarpus***, ***Riccia*** (Figure 52), and ***Targionia*** (Figure 70). But larger thalli in the **Aytoniaceae** [***Asterella*** (Figure 71), ***Mannia*** (Figure 72), ***Reboulia*** (Figure 73)] also exhibit desiccation tolerance (Vitt *et al*. 2014). Much of this tolerance may be structural. For example, these genera typically roll their edges to avoid desiccation. Their pegged rhizoids serve as water conduits and help them to resist desiccation in periodically dry habitats by providing capillary spaces [*e.g.* ***Mannia***, ***Plagiochasma*** (Figure 74), ***Targionia***] (Duckett *et al*. 2014). On the other hand, liverworts from moist habitats tend to be drought intolerant (Figure 69). These include genera with thin thalli such as ***Pellia*** (Figure 75), ***Fossombronia*** (Figure 76), ***Moerckia*** (Figure 77), ***Pallavicinia*** (Figure 78), and ***Symphyogyna*** (Figure 79). Likewise, the primitive genera of ***Haplomitrium*** (**Haplomitriidae;** Figure 80), ***Treubia*** (**Treubiidae;** Figure 81), and ***Apotreubia*** (**Treubiidae**) all grow on constantly moist soil and are drought intolerant (Wood 2007).

Figure 67. ***Corsinia coriandrina***, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.

Figure 68. ***Exormotheca pustulosa***, member of a genus with thick thalli and short life cycles. Photo by Michael Lüth, with permission.

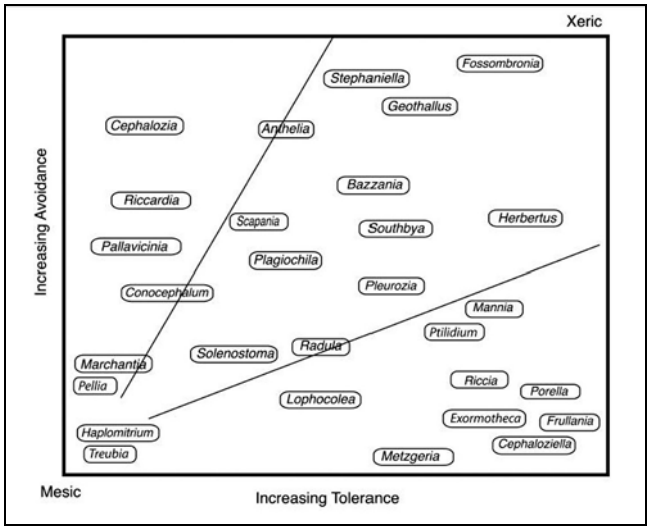

Figure 69. Comparison of liverwort genera with desiccation tolerance vs those with avoidance. Many species of ***Riccia*** are able to use the escape strategy by going dormant to avoid desiccation. From Vitt *et al*. 2014.

Figure 70. ***Targionia lorbeeriana***, member of a genus with thick thalli and short life cycles. Note the black marsupia visible from the ventral side of the thalli. Photo by Michael Lüth, with permission.

Figure 71. ***Asterella saccata***, a large thallus with desiccation tolerance. Photo by Jan-Peter Frahm, with permission.

Figure 72. ***Mannia fragrans***, a large thallus with desiccation tolerance. Note how it rolls as it dries. Photo by Michael Lüth, with permission.

Figure 73. ***Reboulia hemisphaerica***, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.

Figure 74. ***Plagiochasma appendiculatum***, a large thallus with desiccation tolerance. Photo by Michael Lüth, with permission.

Figure 75. ***Pellia epiphylla***, member of a genus with thin thalli that are desiccation intolerant. Photo by David T. Holyoak, with permission.

Figure 76. ***Fossombronia caespitiformis***, member of a genus with thin thalli that are desiccation intolerant. Photo by Des Callaghan, with permission.

Figure 77. ***Moerckia blyttii***, member of a genus with thin thalli that are desiccation intolerant. Photo by Michael Lüth, with permission.

Figure 78. ***Pallavicinia lyellii***, member of a genus with thin thalli that are desiccation intolerant. Photo by Jan-Peter Frahm, with permission.

Figure 79. ***Symphyogyna brasiliensis*** female plant, member of a genus with thin thalli that are desiccation intolerant. Photo by George J. Shepherd, through Creative Commons.

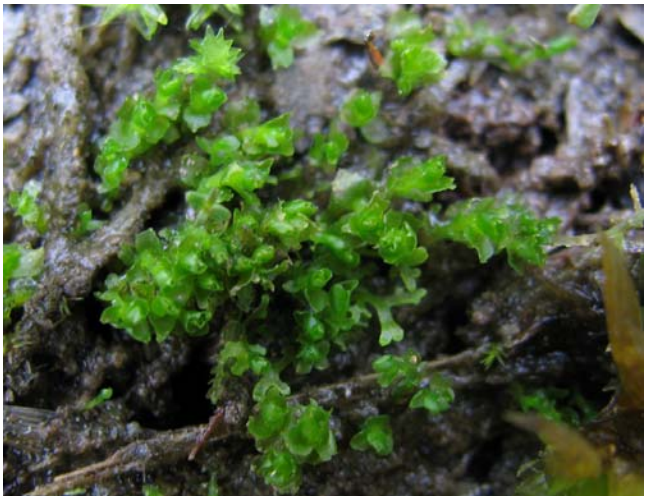

Figure 80. ***Haplomitrium hookeri***, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Janice Glime.

Figure 81. ***Treubia*** sp, a desiccation-intolerant bryophyte of damp or wet habitats. Photo by Jan-Peter Frahm, with permission.

Volk (1984) elucidated the behavior of the genus ***Riccia*** in these flood plain circumstances in Namibia. These are seasonally very dry habitats and members of the genus ***Riccia*** are very common. In this genus, the dorsal (upper) surface is unable to take in water. The ventral surface can absorb water through capillary action among rhizoids and scales, and in some cases hairs. During the dry period, they roll their thalli, exposing these rhizoids and scales from the ventral surface. This rolling thus facilitates the uptake of water from rainfall when it first occurs. These perennial species are very drought resistant and can survive up to seven years with no new water input. They are able to endure heat to greater than 80°C when dry, whereas temperatures above 50°C injure wet plants. They are unable to compete with other plants, but annual species survive by producing large numbers of spores. Perennial species produce fewer spores and survive primarily by going dormant.

Arctic and Antarctic

Kennedy (1993) asked "What limits the presence, distribution, and abundance of life in Antarctica?" To this question he answered that isolation restricts arrival and the paradigm has been that the extreme cold limits survival. But he challenges the latter tenet, suggesting that instead it is moisture that limits the organisms on vertical, horizontal, and temporal scales. Gradients in meltwater, seepage, and upwelling create moisture differences on a continental scale.

Antarctic communities, in particular, experience physiological extremes in water availability and bryophytes must survive both desiccation and submergence (Wasley *et al*. 2006). Growth rate is slow (mean for 17 yrs was 3.7 g dw m^{-2} y^{-1}) (Kanda 1986), providing limited opportunity to compensate for losses during drying. Exposure accounts for the loss of bryophyte flora in many circumstances. This can be particularly true in Arctic climates. Flock (1978) found that acrocarpous mosses dominated in areas with only light snow cover, but in areas with deep snow the pleurocarpous mosses were more abundant. The reason for this is unclear, but one might hypothesize that pleurocarpous mosses are less likely to suffer apical damage from the heavy snow, and even if they do, they usually have numerous growing points to permit their continuation. In this seasonally arid climate, primarily soil moisture and slope account for the distribution of moss communities (LaFarge-England 1989).

At Wilkes Land, Antarctica, colonies of ***Bryum algens*** with a dense tomentum of rhizoids held significantly more water than those with sparse rhizoids (Lewis Smith 1988). In ***Schistidium antarcticum***, the dense shoot arrangement facilitates its high water-holding capacity in the turf form, whereas when this species has less densely packed shoots and thicker cell walls in xeric cushions it maintains a lower water content. On the other hand, the loss of water was much faster in the turf form and the tomentose form of ***Bryum algens***, but this relationship was reversed when it was expressed as a percentage of the initial water content. The mosses take several times longer to reach minimal water conditions when compared to the lichens.

Some mosses form large mounds on the Antarctic terrain. Robinson *et al*. (2000) were able to demonstrate the relationship of desiccation tolerance to habitat in three of these moss species. ***Schistidium antarcticum*** (Figure 82), limited to relatively wet sites, had the least ability to sustain photosynthesis during desiccation. The worldwide ***Ceratodon purpureus*** (Figure 83) had the most and inhabited the driest sites. Intermediate in tolerance was ***Bryum pseudotriquetrum*** (Figure 84), which occupied intermediate habitats and exhibited the greatest plasticity of the three. These responses fit their typical habitat distribution, with ***Ceratodon purpureus*** being common in the driest sites and ***Schistidium. antarcticum*** living in relatively wet sites. Following desiccation, ***Bryum pseudotriquetrum*** contains **stachyose**, a soluble carbohydrate known to provide desiccation tolerance to seeds.

Figure 82. ***Schistidium antarcticum***, a moss limited to relatively wet sites. Photo by Rod Seppelt, with permission.

By contrast, ***Ceratodon purpureus*** has poor survival when it is submerged (Wasley *et al*. 2006). The wet habitat ***Schistidium antarcticum***, on the other hand, has high submersion tolerance. ***Bryum pseudotriquetrum*** (Figure 84) is an intermediate species that is able to co-exist with both of these species and has flexible responses.

Davey (1999) summed up the Antarctic situation by stating that mosses from hydric habitats had lower carbohydrate and higher protein, nitrogen, and phosphorus content than species from drier habitats, suggesting that the

constant flushing provided nutrients. This emphasizes another aspect of the importance of both water and physical factors in the success of Antarctic mosses.

Figure 83. ***Ceratodon purpureus***, the moss with the greatest ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al*. (2000). Photo Rod Seppelt, with permission.

Figure 84. ***Bryum pseudotriquetrum***, the moss with intermediate ability to sustain photosynthesis during desiccation in the Antarctic study of Robinson *et al*. (2000). Photo by Rod Seppelt, with permission.

Are the responses of Antarctic species different from those of other habitats? Apparently not very. Davey (1997) examined effects of various desiccation regimes on photosynthesis of 14 bryophyte species. Using testing intervals of 6 months and 12 months of desiccation, Davey found that the photosynthetic rate decreased as the length of dehydration period increased in all these species. The xeric species had greater retention of photosynthetic rate than did the hydric species, but even the hydric species retained some photosynthesis. Repeated cycles of wet/dry do more harm than continuous dehydration to the hydrophytic species, but the mesophytic and xerophytic species show the opposite response, suggesting that the mesophytic and xerophytic species were able to recover better during short periods of hydration. As the season progresses from spring to autumn, the percentage loss of photosynthetic rate following dehydration/rehydration increases, and this change is most evident in the hydrophytic species. At the same time, it appears that the long winters with concomitant water stress have driven these species to similar adaptations to those of some desert species.

Longton (1988a) concluded that phenotypic plasticity, opportunistic responses in CO_2 exchange, and a poikilohydric water strategy endowed the polar bryophytes with their considerable frost and desiccation tolerance. But he was quick to point out that this plasticity was not unique to polar bryophytes, but rather was common among bryophytes in general. To really understand polar adaptations we need to do physiological studies on the **endemic** (restricted to a certain area) species.

Bryophytes and water level are intimately related in the Arctic. Where the water table is maintained above the bryophyte surface, marshes develop. Where the water table is high above the permafrost, but remains below the bryophyte surface, fens develop. These moss tundras normally have no standing water and water courses are able to move through them from below the surface, maintaining the fen status. The standing water level is thus the primary factor determining the species alliances in that area. Some species complexes, such as that of the ***Catoscopium nigritum*** community (Figure 85), require a temporary period of desiccation to subsist (Vanderpuye *et al*. 2002).

Figure 85. ***Catoscopium nigritum*** exhibiting its fen community where temporary desiccation is required. Photo by Michael Lüth, with permission.

The role of bryophytes in mediating water in the sub-Arctic is crucial for making climate models that adequately predict the effects of climate change. Using ***Sphagnum fuscum*** and ***Polytrichum piliferum***, Street *et al*. (2012) demonstrated that the model does not adequately predict the effect of turf water content on their primary productivity fluxes.

In subarctic mires, water balance often determines which species will dominate (Sonesson *et al*. 2002). When the codominant mosses ***Sphagnum fuscum*** and ***Dicranum elongatum*** were subjected to increased precipitation, both species increased their growth rate, up to 5 mm per day. ***Sphagnum fuscum*** had a 50% higher response in growth compared to ***Dicranum elongatum***, a species of drier habitats than those of ***S. fuscum***. In winter, the responses were affected by the neighboring plants. ***Sphagnum fuscum*** grew better when it was next to ***Dicranum elongatum***, but ***D. elongatum*** also did better when next more ***D. elongatum***.

In the Arctic tundra, Rixen and Mulder (2005) found that high moss species diversity increased productivity, especially in low-density plots, when the plots were

watered regularly. Furthermore, moisture retention was greater in plots with high species richness. Furthermore, plant height was greater in mixed cultures than in single-species cultures. Likewise, 10 out of 12 species grew better in mixture than in monoculture when the density was high and droughts were short. It is interesting that this is the opposite of the relationships found in temperate moss communities.

As suggested by the Antarctic species discussed above, growth form is important in these cold environments that are frequently subjected to water stress. In the subalpine habitat, Nakatsubo (1994) found that large cushions and compact mats were the most common among the xerophytic species. The mesophytic species of the coniferous forest, by contrast, were smooth mats, wefts, and tall turfs. The relation between evaporation rate per basal area of the moss and dry weight per basal area of the colony correlated closely with the growth form. Nakatsubo concluded that the difference in the evaporation rate per weight between the xerophytic and mesophytic species was largely due to the difference in dry weight per basal area of the colony, and that the growth forms of the xerophytic species were suitable for increasing dry weight per basal area of the colony without increasing surface roughness. Increasing surface roughness would lead to an increase in evaporation rate due to increased exposed surface area and increased air turbulence.

Forest Floor

The forest floor would seem to be the most straight-forward and familiar habitat for most of us who have lived our lives in the temperate zone and who hunt mosses. But water relations in this habitat are not so simple. Bryophytes may actually deprive the trees of water in several ways.

In her collections of water samples under moss mats and without moss mats in a Jack pine forest (*Pinus banksiana*), Scafone (unpublished data) found that there were many occasions when 1-2 cm of water accumulated in the collectors with no moss, but the collectors under the moss mats were dry. This means the soil does not receive any of the throughfall during short or light rainfall events where there is a substantial moss mat on the surface. Such a cover is common in boreal and pine forests, depriving upper fine roots of much needed moisture.

But it appears that mosses can even derive their moisture at night from the soil. Carleton and Dunham (2003) accounted for moisture available to mosses during dry summer weather by explaining nocturnal cooling on the forest floor. Cooling of the soil surface at night was sufficient to bring the moss to dew point, reversing the daytime temperature gradient in the forest floor organic profile. By using a vapor barrier for comparison, they determined that the soil provides an upward movement of water at night that permits moss shoots to survive summer "dry-downs." This happens most noticeably in late summer when organic layers have accumulated the most warmth.

Temperate Epiphytes

Epiphytes are subjected to feast or famine for their water needs. In the growing season, they can get flooded by stem flow and may grow best on the side of the tree that gets better stem flow. In the winter they often remain exposed, unprotected by snow, and subject to the harsh, dry winds.

Trynoski and Glime (1982) demonstrated the apparent role of winter when they mapped the locations of epiphytic bryophytes in a northern deciduous forest in the Keweenaw Peninsula of Michigan, USA. The highest cover at the base was on the north side of the tree, but contrary to popular belief, midway between the base and breast height it was greatest on the south side. They attributed this southern location to the drying winds from the north and a safe haven in the space between the tree trunk and the snow that provided a moist microcosm where sufficient sun could penetrate through the snow to permit photosynthesis in winter.

Where winters are not in a constant state of snow cover, they may afford a better growing season for epiphytes due to cooler temperatures and fewer dry days. In British woods, Pitkin (1975) found that most of the growth of the epiphytes ***Hypnum cupressiforme*** (Figure 86) and ***Platygyrium repens*** (Figure 87) occurred in autumn and winter. A similar pattern of growth was found for epiphytes at a second location, and growth periods in both locations corresponded with greater moisture. When summers were wet, the winter growth did not increase proportionally to the summer increase. In wetter climates, temperature and day length have greater importance in determining growth rates.

Figure 86. ***Hypnum cupressiforme***, a species that grows mostly in winter in British woods. Photo by Michael Lüth, with permission.

Figure 87. ***Platygyrium repens*** with bulbils, a species that grows most in autumn and winter in British woods. Photo by Michael Lüth, with permission.

Wu *et al*. (1987) found that epiphyllous liverworts in southeast China required about two hours of direct light and ten hours of diffuse light in winter, with light, temperature, and humidity being the primary factors to control their distribution.

Tropics, Rainforests, and Cloud Forests

Cloud forest (Figure 88) and rainforest bryophytes can experience a wide range of water status in a single 24-hour period (Zotz *et al*. 1997). In a submontane tropical rain forest in Panama, both low and high water content limited carbon gain significantly on a daily basis for bryophytes exhibiting a variety of life forms. More than half of the daily carbon gain (mean 2.9 mg C per g plant) is lost through respiration at night.

Figure 88. ***Macromitrium*** habitat on a tree in a New Zealand cloud forest. Photo by Vita Plasek, with permission.

Although we are beginning to understand the broad aspects of tropical bryophyte ecology, understanding of their physiology has been hampered by taxonomic difficulties and remoteness of the study site from most of the research labs. Hence, only a few studies exist on their desiccation tolerance (*e.g.* Renner 1933; Biebl 1964a, b).

Johnson and Kokila (1970) reviewed desiccation responses in primitive photosynthetic organisms and surmised that in the algae, accumulation of fat in cells, thickening of the cell walls, and accumulation of mucilage can facilitate desiccation resistance. Other characters that correlate with resistance in some algae include resistance to plasmolysis in a hypertonic solution, rigid and viscous protoplasm, and more abundant granules. But in the mosses ***Bryum*** (Figure 1) and ***Mnium*** (Figure 40) the viscosity decreased during drying. Hence, Johnson and Kokila considered how applicable these attributes might be to the desiccation tolerance of tropical bryophytes. They examined ten species that represented a wide range of habitats and exhibited a number of structural adaptations that might contribute to survival of drought.

Some species exhibit damage near the tips, with damage spreading slowly to the lower leaves, and others experience more apparent damage near the base (Johnson & Kokila 1970). The species they studied fell into two groups that mostly coincided with this pattern of damage progression:

Low resistance to desiccation:
(those with * have damage near the tips):
Calymperes moluccense*
Fissidens crassinervis
Leucobryum sanctum*
Semibarbula orientalis*
Syrrhopodon loreus*

High resistance to desiccation:
Bryum coronatum (Figure 89)
Leucophanes octoblepharioides (Figure 93)
Neckeropsis lepineana (Figure 94)
Paraleucobryum longifolium (Figure 95)
Pelekium velatum

Figure 89. ***Bryum coronatum*** surviving on an exposed rock. Photo by Michael Lüth, with permission.

In the tropics, epiphytes can experience long periods of drought during the dry season. Salazar Allen (1985) found that the genus ***Leucophanes*** (Figure 90) survives the drought by an unusual life form strategy. ***Leucophanes*** is an acrocarpous moss that may be branched or unbranched and that forms turfs. The unusual feature is that leaf-tip gemmae germinate on the parent plant to form a new layer of gametophores (Figure 91). In many bryophytes, there seems to be an inhibitory substance that prevents such occurrences (see interaction chapter). However, in ***Leucophanes***, this seems to be an important adaptation for water retention. Lacking subterminal innovations, ***Leucophanes*** benefits from the thicker turf where the numerous stems can protect each other from drying out. It is my guess that if the tips were to become so dry that they would die in an unusually dry year, there would be at least some lower (older) stems with enough life remaining to re-establish the colony. If not, surely some of the gemmae would survive. In any event, this habit of germination of gemmae within the parent colony provides ***Leucophanes*** with a dense turf that could resist drying.

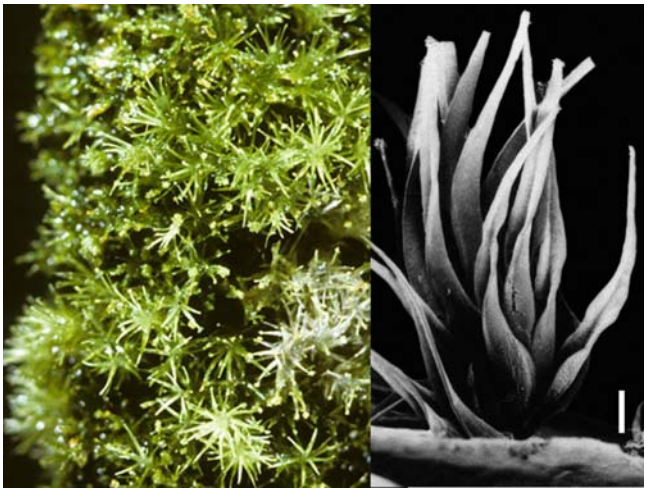

Figure 90. ***Leucophanes molleri*** on tree bark. **Left:** showing plants with leaves tipped with gemmae and **Right:** gemmae on leaf tip. Bar = 20 µm. Photos courtesy of Noris Salazar Allen.

Figure 91. Protonemata forming at the tip of a gemma of ***Leucophanes molleri*** while the gemma is still attached to the parent leaf. Photo courtesy of Noris Salazar Allen.

Among those adapted for drying, with little damage down to 10% humidity, ***Leucophanes octoblepharioides*** (Figure 93) has abundant leucocysts that serve as a water reservoir (Johnson & Kokila 1970). The costa is thickened and prevents the leaf from collapsing. ***Paraleucobryum longifolium*** (Figure 95), a species of exposed situations in the hill forest, has a thickened costa and thick-walled lamina cells. ***Pelekium velatum*** (Figure 92) uses a different strategy with very small leaves pressed against the stem and with papillose cells. ***Neckeropsis lepineana*** (Figure 94) holds its secondary branches at an angle to the tree trunk in a way that subjects it to drying.

Those species with low desiccation resistance are damaged at humidity of 63% and are likely to die at 10% (71-94% of cells damaged) (Johnson & Kokila 1970). These species live in habitats that have near saturation humidity levels. Three of these species live on the ground where the humidity is constantly and exceedingly high. Two are **corticolous** (growing on bark) species [***Calymperes moluccense*** (Figure 96) and ***Syrrhopodon loreus***) that live on the wettest side of the tree in areas that are constantly wet due to runoff.

Figure 92. ***Pelekium velatum***, a species with very small leaves and papillae. Photo © <www.NatureLoveYou.sg>, with online permission.

Figure 93. ***Leucophanes*** sp. ***Leucophanes octoblepharioides*** has low resistance to plasmolysis and is shown here surviving on bark. Photo by Niels Klazenga, with permission.

Figure 94. ***Neckeropsis lepineana*** surviving on bark with its branches extended – a common growth form in the tropics. Photo by Li Zhang, with permission.

Figure 95. ***Paraleucobryum longifolium*** on rock, a species adapted for drying by a thickened costa and thick-walled lamina cells. Photo by Janice Glime.

Figure 96. Saturated ***Calymperes*** sp. ***Calymperes moluccense*** lives on the wettest sides of trees in humid areas and is desiccation intolerant. Photo by Niels Klazenga, with permission.

Pardow and Lakatos (2013) explored the desiccation tolerance of epiphytic bryophytes from contrasting microsites in tropical lowland forests of French Guiana. Canopy species are well adapted, as indicated by the recovery of chlorophyll fluorescence, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after 9 days at 43% relative humidity. On the other hand, understory species were sensitive to desiccation and were only able to withstand a reduction to 75% relative humidity. The bryophytes were able to reactivate by reaching equilibration with water vapor as their only moisture source.

Pardow *et al*. (2012) noted the importance of lowland cloud forests in the Guianas as a site for high epiphytic bryophyte diversity. This area is subject to frequent early morning fog events that provide moisture for the bryophytes. The growth forms were those that could take greatest advantage of this cloud moisture: tail, weft, and pendent (Figure 97).

Figure 97. ***Papillaria***, a pendent moss in the cloud forest at Mt. Budawang, Australia. Photo by Peter Woodard, through Public Domain

Romanski *et al*. (2011) likewise studied epiphytes, in this case in the lower montane (2400 m) rainforest of Peru. A single tree of *Weinmannia* supported 110 bryophyte species (77 hepatics, 1 hornwort, 32 mosses). They divided the tree into **Johansson zones** (lower trunk, upper trunk, mid-crown, mid-outer crown, outer crown) and found the greatest species richness and abundance on the upper trunk and large branches of the mid-crown. Exposure to light and desiccation appeared to account for the bryophyte distribution, but more research is necessary to tease out these relationships.

Atala *et al*. (2013) expressed concern that dendroid mosses with conducting tissues likewise lacked study. They examined desiccation tolerance in the ***Dendroligotrichum dendroides*** (Figure 98) from Chile, where it grows in the understory of temperate forests. They tested plants from two contrasting moisture conditions and found that both populations exhibited desiccation tolerance. But the responses wee not equal. Those from the northern population lost water more slowly and recovered the PSII Fv/Fm to higher values when compared to the southern population. They suggested that exposure to summer droughts in the northern population could contribute to differences in their response.

Figure 98. ***Dendroligotrichum dendroides***, a Chilean species with desiccation tolerance. Photo by Felipe Osorio-Zúñiga, with permission.

Epiphytes

Epiphytes in most habitats have sharply contrasting moisture conditions. When it rains, they can be in a river of water rolling down the tree trunks. But when the rain stops, they are elevated where there is more access to wind and drying can be rapid.

These conditions are not so severe in a cloud forest due to the moisture in the clouds. Bryophytes are able to use such moisture and some are even adapted to collect it by providing fine wirelike structures, expressed as such structures as thin awns or pendent growth forms.

In two Venezuelan cloud forests, León-Vargas *et al*. (2006) the rainfall averages only 20 mm or less in January and February, 200 mm or more in August to October, and variable year-round. Continuous 100% relative humidity occurred 8.5% to 52.2% of the time. Humidity increased at night. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All of the six pendent bryophyte species survived at least a few days of desiccation.

Pendent Mosses

Pendent mosses (those that hang down; Figure 99-Figure 100) often suffer desiccation, with little surrounding them to help hold in the water. ***Floribundaria floribunda*** (Figure 99) and ***Pilotrichella ampullacea*** (Figure 100) from Uganda humid tropical forests survive partly by avoidance, holding large quantities of external capillary water, with ***Pilotrichella ampullacea*** holding approximately twice as much as ***Floribundaria floribunda*** (Proctor 2002). Both species were able to recover from 11 months of dry storage at 5°C, although they required several days to recover, with ***F. floribunda*** recovering more slowly and less completely. Following 20 hours of air drying, ***P. ampullacea*** achieved a positive carbon balance within 30-60 minutes after rewetting.

Figure 99. ***Floribundaria floribunda***, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.

León-Vargas *et al.* (2006) studied the epiphytes in the Venezuelan cloud forests. The rainfall there drops to an average of 20 mm or less in January and February and increases to 200 mm or more from August to October. Nevertheless, the longest recorded dry period was only 143 hours. Nighttime humidities of 90% relative humidity were common, with 100% for significant periods, creating cloud water deposition in about 50% of the nights. Although these cloud forests are among the most ideal for epiphytic bryophytes, even they can have short periods droughts at any time of year. They noted that the pendent life form was probably important in harvesting the moisture from the air in these forests. All six species of pendent bryophytes survived for at least a few days of desiccation; these recovered better from high than from low humidities.

Altitude Differences in the Tropics

In the tropics, altitude can have a strong effect on both biomass and diversity among bryophytes (Bader *et al.* 2013). The lowlands are characterized by low abundance and low species richness. These could be a consequence of short daily periods of suitable light, temperature, and moisture and nighttime high respiration due to high temperatures. Moisture regimes are quite different, with lowland forests having more concentrated but less frequent precipitation than montane cloud forests. they furthermore have sunny mornings that cause rapid drying. The high levels of moisture in high altitude cloud forests is manifest in a high diversity and cover by bryophytes (Figure 101). But both lowland and montane species are able to survive more than 80 days of dry periods, far exceeding the duration of lowland tropical dry periods.

Figure 100. ***Pilotrichella ampullacea***, a species from humid forests in Uganda that survives partly by avoidance, holding large quantities of external capillary water. Photo by Jan-Peter Frahm, with permission.

Figure 101. Elfin cloud forest in the Luquillo Mountains of Puerto Rico. Photo by Janice Glime.

Summary

Because of their small size, bryophytes are able to occupy microsites in otherwise unfavorable habitats. Their ability to recover from dehydration typically correlates with habitat, with aquatic bryophytes having little ability to tolerate dehydration and resume photosynthesis, whereas dry habitat bryophytes can withstand extended periods of desiccation. In aquatic bryophytes, ribosomes can be damaged irreversibly and membranes are more likely to be damaged than in dry habitat taxa. On the other hand, there is no difference in nitrogen reductase activity between dry and wet habitat bryophytes.

Peatland bryophytes (***Sphagnum***) of lawns and hollows are typically desiccation tolerant, benefitting from inducible tolerance. Those of hummocks generally are intolerant but are desiccation resistant. Submersed species rely on the water of their habitat and have little tolerance for desiccation.

Aquatic bryophytes have poor desiccation tolerance, especially with rapid drying, but usually benefit from slow drying and sometimes can survive considerable dry periods.

A number of bryophytes are xerophytic. Their life cycle is typically short and the strategy is adapted to the short periods of rainfall. But in some arid habitats, nighttime dew is the only source of water for bryophytes. Hair points gather the dew and facilitate its uptake. In others, cooling of soil can bring bryophytes to dew point and draw water upward from the soil. The real limiting factor is carbon balance. If the bryophyte loses too much carbon by respiration and experiences a hydrated state for which the duration is too short to recover it, the bryophyte will perish. Rapid repair and recovery of photosynthesis permit these bryophytes to take advantage of short periods of hydration. The rapid daytime drying makes constitutive desiccation tolerance essential for survival where short daytime storms are common. But at least some of these bryophytes also have inducible desiccation tolerance. Some use an **escape strategy** of desiccation-tolerant gemmae, spores, and protonemata that help these bryophytes succeed in habitats with extensive dry periods. Nitrite and nitrate reductase both seem to be involved in recovery, but more research is need to determine the mechanisms involved. Leaf rolling and papillae seem to provide a protective role, perhaps by reducing light damage of dry cells and facilitating water uptake, but their role in water retention remains to be demonstrated. Compact growth form is also important.

Flood plains have extremes of habitat and require special strategies to weather these. Many of the bryophytes adapted to these extremes are species of the thallose liverwort ***Riccia***. This genus is able to go dormant when it is dry with a variety of strategies, including rolling the thallus, surviving as tubers, having hairs on the surface. Some have small thalli with short life cycles; others have thick thalli that survive the desiccation.

In the Arctic and Antarctic, frost can be a desiccant. Water height above permafrost determines existence of fens, where bryophytes are emergent, and marshes exist where the water table is high above the bryophyte surface. Arctic bryophytes suffer from exposure that creates desiccating conditions. Aspect and angle of slope play important roles in speed and frequency of drying. Acrocarpous mosses do better in areas of light snow cover, whereas pleurocarpous mosses suffer less apical damage from heavy snow. In the Antarctic, the longer the dry period, the lower the subsequent photosynthetic rate, especially among hydrophytic species.

On the forest floor, bryophytes may sequester all the water from a brief rainfall (1-2 cm). In the dry summer, bryophytes may derive moisture from the soil during the cooling temperatures.

Temperate epiphytes may take advantage of cooler temperatures of winter for maximum growth.

In the tropics, carbon balance can, as in the desert, be a problem. When the mosses are hydrated at higher temperatures, respiration loss exceeds photosynthetic gain. This is generally not a problem at higher altitudes in the cloud forests; bryophytes are abundant on nearly every substrate there. Physiology is poorly known for tropical bryophytes, but it appears that they have similar adaptations to those of other locales with similar moisture conditions such as thick costa and thick cell walls. Some (***Leucophanes***) have leaf-tip gemmae that germinate and layer the colony, making a thick turf.

Acknowledgments

This chapter benefitted from Beth Scafone and Medora Burke-Scoll, who offered helpful comments on the text. Jean Faubert provided helpful comments and suggestions.

Literature Cited

Alpert, P. 1979. Desiccation of desert mosses following a summer rainstorm. Bryologist 82: 65-71.

Alpert, P. 1982. Poikilohydry and desiccation tolerance in some xerophytic mosses. Ph. D. Dissertation, Harvard University, Cambridge. pp. 19-31.

Alpert, P. 1985. Distribution quantified by microtopography in an assemblage of saxicolous mosses. Vegetatio 64: 131-139.

Alpert, P. 1988. Survival of a desiccation-tolerant moss, *Grimmia laevigata*, beyond its observed microdistributional limits. J. Bryol. 15: 219-227.

Alpert, P. and Oechel, W. C. 1985. Carbon balance limits the microdistribution of *Grimmia laevigata*, a desiccation-tolerant plant. Ecology 66: 660-669.

Atala, C., Alfaro, J. F., Parra, M. J. and Saldaña, A. 2014. Desiccation tolerance in *Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. from two Chilean populations with contrasting precipitation. Guyana Bot. 71: 10-16.

Bader, M. Y., Reich, T., Wagner, S., González, A. S., and Zotz, G. 2013. Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. J. Bryol. 35: 47-56.

Bates, J. W., Roy, D. B., and Preston, C. D. 2004. Occurrence of epiphytic bryophytes in a 'tetrad' transect across southern Britain. 2. Analysis and modelling of epiphyte-environment relationships. J. Bryol. 26: 181-197.

Bewley, J. D. 1974. Protein synthesis and polyribosome stability upon desiccation of the aquatic moss *Hygrohypnum luridum*. Can. J. Bot. 52: 423-427.

Bewley, J. D. and Gwozdz, E. A. 1975. Plant desiccation and protein synthesis II. On the relationship between endogenous adenosine triphosphate levels and protein-synthesizing capacity. Plant Physiol. 55: 1110-1114.

Biebl, R. 1964a. Austrocknungsresistenz tropischer Pflanzen auf Puerto Rico. Protoplasma 59: 133-156.

Biebl, R. 1964b. Austrocknungsresistenz tropischer Urwaldmoose auf Puerto Rico. Protoplasma 59: 277-297.

Bischler, H. 1998. Systematics and evolution of the genera of the Marchantiales. Bryophytorum Bibliotheca 51: 1-201.

Brown, D.H. and Buck, G. W. 1979. Desiccation effects and cation distribution in bryophytes. New Phytol. 82: 115-125.

Brown, D. H. and Mahmood, S. 1996. Observations on the histochemical localization of intracellular potassium in *Mnium hornum*. J. Bryol. 19: 361-365.

Carleton, T. J. and Dunham, K. M. M. 2003. Distillation in a boreal mossy forest floor. Can. J. Forest Res. 33: 663-671.

Carvalho, R. C. de, Branquinho, C., and Silva, J. M. da. 2011. Physiological consequences of desiccation in the aquatic bryophyte *Fontinalis antipyretica*. Planta 234: 195-205.

Crandall-Stotler, B. J. and Bozzola, J. J. 1990. Ultrastructural details of leaf papilla development in the moss *Andreaeobryum macrosporum*. Proceedings of the XIIth International Congress for Electron Microscopy, San Francisco Press, Inc., CA, pp. 670-671.

Crandall-Stotler, B. J., Stotler, R. E., and Doyle, W. T. 2006. On *Anthoceros phymatodes* M. Howe and the hornwort genus *Phymatoceros* Stotler, W. T. Doyle & Crand.-Stotl. (Anthocerotophyta). Cryptog. Bryol. 27: 59-73.

Cruz de Carvalho, R., Silva, A. B., Soares, R., Almeida, A., Coelho, A. V., Marques da Silva, J., and Branquinho, C. 2014. Differential proteomics of dehydration and rehydration in bryophytes: Evidence towards a common desiccation tolerance mechanism. Plant Cell Environ. 37: 1499-1550.

Davey, M. C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25-31.

Davey, M. C. 1999. The elemental and biochemical composition of bryophytes from the maritime Antarctic. Antarct. Sci. 11: 157-159.

Di Nola, L., Mayer, A. M., and Heyn, C. C. 1983. Respiration, photosynthesis and drought tolerance in mosses from various habitats in Israel. Israel J. Bot. 32(4): 189-202.

Duckett, J. G., Ligrone, R., Renzaglia, K. S., and Pressel, S. 2014. Pegged and smooth rhizoids in complex thalloid liverworts (Marchantiopsida): Structure, function and evolution. Bot. J. Linn. Soc. 174: 68-92.

Flock, J. A. W. 1978. Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. Arct. Alp. Res. 10: 31-47.

Frey, W. and Kürschner, H. 1991. Morphologische und anatomische Anpassungen der Arten in terrestrisschen Bryophytengesellschaften entlang eines ökologischen Gradienten in der Judäischen Wüste. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 112: 529-552.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Nat. 111: 1169-1195.

Hájek, T. and Vicherová, E. 2013. Desiccation tolerance of *Sphagnum* revisited: A puzzle resolved. Plant Biol. 16: 765-773.

Hartung, W., Hellwege, E. M., and Volk, O. H. 1994. The function of abscisic acid in bryophytes. J. Hattori Bot. Lab. 76: 59-65.

Hébrard, J.-P. and Rolando, C. 1985. Etude comparee de peuplement bryophytique de taillis de chene vert d'age different en foret dominiale de la Gardiole de Rians (Var, France). Ecologia Mediterranea 11(2/3): 87-110.

Herrnstadt, I. and Kidron, G. J. 2005. Reproductive strategies of *Bryum dunense* in three microhabitats in the Negev Desert. Bryologist 108: 101-109.

Hettenbergerova, E., Hajek, M., Zeleny D., Jirouskova, J., and Mikulaskova, E. 2013. Changes in species richness and species composition of vascular plants and bryophytes along a moisture gradient. Preslia 85: 369-388.

Irmscher, E. 1912. Über die Resistenz der Laubmoose gegen Austrocknung und Kalte. Jahr. Wiss. Bot. 50: 387-449.

Johnson, A. and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. Bryologist 73: 683-686.

Kanda, H. 1986. Seasonal changes of some environmental factors around the moss vegetation near Syowa Station, east Antarctica. Mem. Natl. Inst. Polar Res. Ser. E Biol. Med. Sci. 37: 17-26.

Kappen, L., Lange, O. L., Schulze, E. D., Evenari, M., and Buschbom, U. 1979. Ecophysiological investigations on lichens of the Negev desert. 6. Annual course of photosynthetic production of *Ramalina maciformis* (Del.) Bory. Flora Jena 168: 85-108.

Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. Arct. Alp. Res. 25: 308-315.

Krupa, J. 1977. The interdependence between transpiration intensity and the anatomical structure of moss leaves. Acta Soc. Bot. Polon. 66 (1): 57-68.

LaFarge-England, C. 1989. The contemporary moss assemblages of a high Arctic upland, northern Ellesmere Island, N.W.T., Canada. Can. J. Bot. 67: 491-504.

Lange, A. 1955. Untersuchungen über die Hitzeresistenz der Moose in Beziehung zur ihrer Verbreitung. I. Die Resistenz stark ausgetrockneter Moose. Flora Jena 142: 381-399.

León-Vargas, Y., Engwald, S., and Proctor, M. C. F. 2006. Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. J. Biogeogr. 33: 901-913.

Lewis Smith, R. I. 1988. Aspects of cryptogam water relations at a continental Antarctic site. Polarforschung 58: 139-153.

Longton, R. E. 1979. Climatic adaptation of bryophytes in relation to systematics. In: Bryophyte Systematics, Systematics Association Special Vol. No. 14, Academic Press, New York, pp. 511-531.

Longton, R. E. 1988a. Adaptations and strategies of polar bryophytes. Bot. J. Linn. Soc. 98: 253-268.

Longton, R. E. 1988b. Life-history strategies among bryophytes of arid regions. J. Hattori Bot. Lab. 64: 15-28.

Mahan, J. R., Oliver, M. J., and Sherman, T. D. 1998. Nitrate reductase activity during desiccation and rehydration of the desiccation-tolerant moss *Tortula ruralis*. Environ. Exper. Bot. 39(1): 67-76.

Marschall, M. 1998. Nitrate reductase activity during desiccation and rehydration of the desiccation resistant moss *Tortula ruralis* and the leafy liverwort *Porella platyphylla*. J. Bryol. 20: 273-285.

Mishler, B. D. and Oliver, M. J. 1991. Gametophytic phenology of *Tortula ruralis*, a desiccation-tolerant moss, in the Organ Mountains of Southern New Mexico. Bryologist 94: 143-153.

Mücher, H. J., Charters, C. J., Tongway, D. J., and Green R. S. B. 1988. Micromorphology and significance of the surface crusts of soils in rangelands near Cobar, Australia. Geoderma 42: 227-244.

Nakatsubo, T. 1994. The effect of growth form on the evaporation in some subalpine mosses. Ecol. Res. 9: 245-250.

Nash, T. H., White, S. L., and Marsh, J. E. 1977. Lichen and moss distribution and biomass in hot desert ecosystems. Bryologist 80: 470-479.

Nörr, M. 1974. Hitzeresistenz bei Moosen. Flora Jena 163: 388-397.

Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. Bot. J. Linn. Soc. 104: 281-291.

Oliver, M. J. and Bewley, J. D. 1984a. Plant desiccation and protein synthesis. IV. RNA synthesis, stability, and recruitment of RNA into protein synthesis during desiccation and rehydration of the desiccation-tolerant moss, *Tortula ruralis*. Plant Physiol. 74: 21-25.

Oliver, M. J. and Bewley, J. D. 1984b. Plant desiccation and protein synthesis. VI. Changes in protein synthesis elicited by desiccation of the moss *Tortula ruralis* are effected at the translational level. Plant Physiol. 74: 923-927.

Pardow, A. and Lakatos, M. 2013. Desiccation tolerance and global change: Implications for tropical bryophytes in lowland forests. Biotropica 45: 27-36.

Pardow, A., Gehrig-Downie, C., Gradstein, S. R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. Biodiv. Conserv. 21: 3637-3655.

Pence, V. C., Dunford, S. S., and Redella, S. 2005. Differential effects of abscisic acid on desiccation tolerance and carbohydrates in three species of liverworts. J. Plant Physiol. 162: 1331-1337.

Pitkin, P. H. 1975. Variability and seasonability of the growth of some corticolous pleurocarpous mosses. J. Bryol. 8: 337-356.

Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman and Hall, London, pp. 333-381.

Proctor, M. C. F. 2002. Ecophysiological measurements on two pendulous forest mosses from Uganda, *Pilotrichella ampullacea* and *Floribundaria floribunda*. J. Bryol. 24: 223-232.

Proctor, M. C. F. 2014. The diversification of bryophytes and vascular plants in evolving terrestrial environment. *PUBL In: Hanson, D. T. and Rice, S. K. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Springer, Dordrecht, pp. 59-77.

Reed, S. C., Coe, K. K., Sparks, J. P., Housman, D. C., Zelikova, T. J., and Belnap, J. 2012. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. Nature Climate Change 2: 752-755.

Renner, O. 1933. Zur Kenntnis des Wasserhaushalts Javanischer Kleinepiphyten. Planta 18: 215-287.

Renzaglia, K. S., Villarreal, J. C., and Duff, R. J. 2009. New insights into morphology, anatomy, and systematics of hornworts. In: Shaw, A. J. and Goffinet, B. (eds.). Bryophyte Biology. 2nd edn. Cambridge University Press, Cambridge, pp. 139-171.

Richardson, D. H. S. 1981. The Biology of Mosses. John Wiley & Sons, Inc., N. Y., 220 pp.

Rivera-Aguilar, V., Godinez-Alvarez, H., Manuell-Cacheux, I., and Rodriguez-Zaragoza, S. 2005. Physical effects of biological soil crusts on seed germination of two desert plants under laboratory conditions. J. Arid Environ. 63: 344-352.

Rixen, C. and Mulder, C. P. 2005. Improved water retention links high species richness with increased productivity in arctic tundra moss communities. Oecologia 146: 287-299.

Robinson, S. A., Wasley, J., Popp, M., and Lovelock, C. E. 2000. Desiccation tolerance of three moss species from continental Antarctica. Austral. J. Plant Physiol. 27: 379-388.

Romanski, J., Pharo, E. J., and Kirkpatrick, J. B. 2011. Epiphytic bryophytes and habitat variation in montane rainforest, Peru. Bryologist 114: 720-731.

Sagot, C. and Rochefort, L. 1996. Tolérance des sphaignes à la dessiccation. Cryptog. Bryol. Lichénol. 17: 171–183.

Salazar Allen, N. 1985. The life-form and presence of epigametophytic plants in the genus *Leucophanes*. Bryologist 88: 94-97.

Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140: 677-684.

Schofield, W. B. 1985. Introduction to Bryology. Macmillan Publ. Co., N.Y., xvi + 431 pp.

Seppelt, R. D. and Laursen, G. A. 1999. *Riccia cavernosa* Hoffm. emend Raddi, new to the Arctic and the bryoflora of Alaska. Hikobia 13: 71-76.

Serpe, M., Orm, J., Barkes, T., and Rosentreter, R. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecol. 185: 163-178.

Sheard, J. W. 1968. Vegetation pattern in a moss-lichen heath associated with primary topographic features on Jan Mayen. Bryologist 71: 21-28.

Šinžar-Sekulić, J., Sabovljević, M., and Stevanović, B. 2005. Poređenje tolerancije isušivanja kod mahovina sa različitih staništa. [Comparison of desiccation tolerance among mosses from different habitats.]. Arch. Biol. Sci. (Belgrade) 57: 189-192.

Skré, O., Oechel, W. C., and Miller, P. M. 1983. Patterns of translocation of carbon in four common moss species in a black spruce (*Picea mariana*) dominated forest in interior Alaska. Can. J. Forest Res. 13: 869-878.

Söderström, L. 1981. Distribution of bryophytes in spruce forests on hill slopes in central Sweden. Wahlenbergia 7: 141-153.

Sonesson, M., Carlsson, B. Å., Callaghan, T. V., Halling, S., Björn, L. O., Bertgren, M., and Johanson, U. 2002. Growth of two peat-forming mosses in subarctic mires: Species interactions and effects of simulated climate change. Oikos 99: 151-160.

Stark, L. R. 2001. Widespread sporophyte abortion following summer rains in Mojave Desert populations of *Grimmia orbicularis*. Bryologist 104: 115-125.

Stark, L. R. 2002. Skipped reproductive cycles and extensive sporophyte abortion in the desert moss *Tortula inermis* correspond to unusual rainfall patterns. Can. J. Bot. 80: 533-542.

Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.

Street, L. E., Stoy, P. C., Sommerkorn, M., Fletcher, B. J., Sloan, V. L., Hill, T. C., and Williams, M. 2012. Seasonal bryophyte productivity in the sub-Arctic: A comparison with vascular plants. Funct. Ecol. 26: 365-378.

Tao, Y. and Zhang, Y. M. 2012. Effects of leaf hair points of a desert moss on water retention and dew formation: Implications for desiccation tolerance. J. Plant Res. 125: 351-360.

Trynoski, S. E. and Glime, J. M. 1982. Direction and height of bryophytes on four species of northern trees. Bryologist 85: 281-300.

Vanderpoorten, A. and Engels, P. 2002. The effects of environmental variation on bryophytes at a regional scale. Ecography 25: 513-522.

Vanderpuye, A. W., Elvebakk, A. and Nilsen, L. 2002. Plant communities along environmental gradients of high-Arctic mires in Sassendalen, Svalbard. J. Veg. Sci. 13: 875-884.

Varo, J., Guerra, J., Zafra, M. L., and Ros, R. M. 1992. Regression and invasion of bryophytes in the south and southeast of the Iberian Peninsula. Biol. Conserv. 59: 129-131.

Vitt, D. H. and Glime, J. M. 1984. The structural adaptations of aquatic Musci. Lindbergia 10: 95-110.

Vitt, D. H., Crandall-Stotler, B., and Wood, A. 2014. Survival in a dry world through avoidance and tolerance. In: Rajakaruna, N., Boyd, R., and Harris, T. (eds.). Plant Ecology and Evolution in Harsh Environments. Nova Publishers, pp. 267-295.

Volk, O. H. 1984. Beiträge zur Kenntnis der Marchantiales in Südwest-Afrika/Namibia. IV. Zur Biologie einiger Hepaticae mit besonderer Berücksichtigung der Gattung *Riccia*. [Contribution to the knowledge of the Marchantiales in Southwest Africa/Namibia. IV. The biology of some Hepaticae with particular consideration of the genus *Riccia*.]. Nova Hedw. 39: 117-144.

Wagner, D. J. and Titus, J. E. 1984. Comparative desiccation tolerance of two *Sphagnum* mosses. Oecologia 62: 182-187.

Wasley, J., Robinson, S., Lovelock, C., and Popp, M. 2006. Some like it wet – biological characteristics underpinning tolerance of extreme water stress events in Antarctic bryophytes. Funct. Plant Biol. 33: 443-455.

Wood, A. J. 2007. The nature and distribution of vegetative desiccation-tolerance in hornworts, liverworts and mosses. Bryologist 110: 163-177.

Wu, L., Zhang, Y., Zhang, J., and Downing, A. 2015. Precipitation intensity is the primary driver of moss crust-derived CO_2 exchange: Implications for soil C balance in a temperate desert of northwestern China. Eur. J. Soil Biol. 67: 27-34.

Wu, P.-C., Li, D.-K., and Gao, C.-H. 1987. Light and epiphyllous liverworts in the subtropical evergreen forests of south-east China. Symp. Biol. Hung. 35: 27-32.

Zhang, J., Zhang, Y.-M., Downing, A., Wu, N., and Zhang, B.-C. 2011. Photosynthetic and cytological recovery on remoistening *Syntrichia caninervis* Mitt., a desiccation-tolerant moss from Northwestern China. Photosynthetica 49: 13-20.

Zotz, G., Budel, B., Meyer, A., Zellner H., and Lange, O. L. 1997. Water relations and CO_2 exchange of tropical bryophytes in a lower montane rainforest in Panama. Bot. Acta 110: 9-17.

CHAPTER 7-9
WATER RELATIONS: WINTER PHYSIOLOGY

TABLE OF CONTENTS

Problems in Winter 7-9-2
Frost Damage 7-9-3
Ice Crystals 7-9-10
Desiccating Conditions 7-9-11
Desiccation Tolerance 7-9-13
Ice-nucleating Proteins 7-9-16
Atmospheric Source 7-9-17
Nucleating Proteins in Lichens 7-9-18
Nucleating Proteins as a Source of Water 7-9-18
Compounds for Winter? 7-9-18
Sugars 7-9-18
ABA 7-9-21
Arachidonic Acid 7-9-22
Polyribosomes 7-9-22
Summary 7-9-22
Acknowledgments 7-9-22
Literature Cited 7-9-22

CHAPTER 7-9
WATER RELATIONS: WINTER PHYSIOLOGY

Figure 1. ***Racomitrium heterostichum*** encased in ice. Photo by Michael Lüth, with permission.

Freezing tolerance must necessarily be coupled with drought tolerance and therefore this chapter would be incomplete without a discussion of winter effects. While other plants are dormant and have either lost their leaves, died back to ground level, or adapted in other ways to prevent damage from heavy snow and loss of water due to ice crystals, many bryophytes remain exposed, ready to have photosynthesis whenever light, water, and temperatures permit (Figure 1). Here we will examine the conditions related to their winter water relations. Temperature relations will be covered in a different chapter.

Problems in Winter

Bryophytes do have problems to deal with in winter. These include damage to their DNA and photosynthetic tissue (chlorophyll) from the UV light, temperature stress, cellular freezing and structural damage, and desiccation damage due to ice crystals. Alberdi *et al*. (2002) consider that adaptations to cold include high resistance to light stress, high freezing resistance, and high photosynthetic capacity at low temperatures. To this list I must add the ability to regain hydration quickly upon thawing. Most of these topics will be discussed elsewhere in chapters that deal with that particular physiological parameter. This chapter will examine the winter water relations.

The all-important water, whether as fog or rain or dew, is suddenly no longer liquid, but solid. Not only does this present problems for obtaining water, but it also means that hygroscopic ice crystals can draw water from the bryophyte cells.

But not all bryophytes suffer from the problem of ice damage. The thallose liverwort ***Ricciocarpos natans*** (Figure 2-Figure 4) can spend the winter encased in ice and can tolerate temperatures to -30°C (Frahm 2006). Frahm suggested that it was able to survive this frozen condition because it has no water vacuoles, thus providing no free internal water to form crystals that could destroy its

membranes. Rod Seppelt (Bryonet discussion 14 November 1997) also noted an absence of vacuoles in Antarctic mosses. Both ***Ricciocarpos natans*** and ***Riccia fluitans*** (Figure 5-Figure 6) are common in Arctic streams, so we might expect them to have this absence of vacuoles. I find it interesting that no one seems to have reported either presence or absence of vacuoles in ***R. natans*** (based on literature search and question posed on Bryonet in April 2015). Rather, lipids and starch bodies may help in their winter tolerance (Rod Seppelt, Bryonet discussion 14 November 1997).

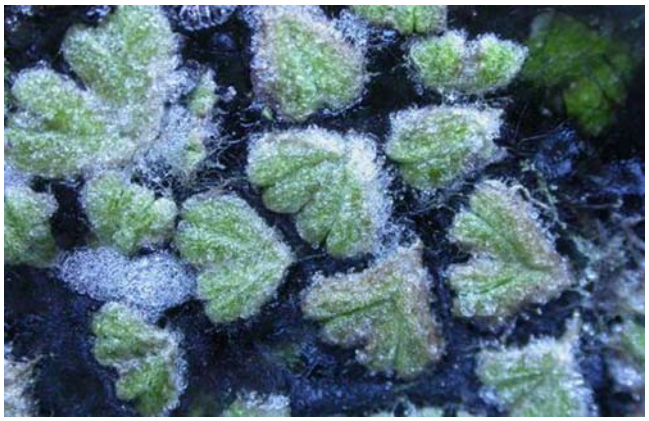

Figure 2. ***Ricciocarpos natans*** in ice. Photo by Jan-Peter Frahm, with permission.

Figure 3. ***Ricciocarpos natans*** thallus, a species with lipids and starch bodies that may help it survive winter. Photo by Norbert Stapper, with permission.

Figure 4. ***Ricciocarpos natans*** section showing the many chambers packed with small chlorophyllose cells. Photo by Norbert Stapper, with permission.

Figure 5. ***Riccia fluitans*** with pearling, a species that survives freezing. Photo by Christian Fischer, with permission.

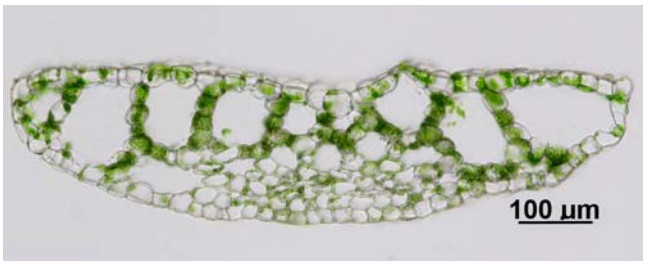

Figure 6. ***Riccia fluitans*** cross section showing large air chambers that help it to float. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Frost Damage

Those venues of green in the spring attest to the survival of bryophytes through the winter, subjected to frost before snow cover arrives and subsisting at near 0°C under the snow. But few studies give us specifics on what species survive and which ones are damaged.

Fletcher (1982) had the opportunity to document the frost responses of a number of species in cultivation. Among the winter survivors, reaching temperatures as low as -3°C, are species from New Zealand [***Papillaria crocea*** (Figure 7), ***Hypopterygium*** spp. (Figure 8), ***Rhizogonium bifarium*** (see Figure 9), ***Cyathophorum bulbosum*** (Figure 10), ***Eriopus brownii***], South Africa [***Hypopterygium*** sp.], Australia [***Gigaspermum repens*** (Figure 11), ***Goniomitrium acuminatum*** subsp. ***enerve*** (=***Goniobryum enerve***; Figure 12)], and Florida, USA [***Rhizogonium spiniforme*** (Figure 13)]. Even the delicate-looking ***Takakia lepidozioides*** (Figure 14-Figure 15) remains healthy. As we might expect, the widespread mosses ***Sphagnum*** spp. (Figure 16) and ***Mnium*** spp. [probably ***Plagiomnium*** since no ***Mnium*** species are present in New Zealand (NZOR 2015); Figure 17] survive the frost. On the other hand, ***Haplomitrium hookeri*** (Figure 18) from New Zealand and ***H. mnioides*** (Figure 19) from Japan had no healthy plants remaining after an exposure to -3°C, despite their ability to survive and grow in the winters in their native habitats.

Figure 7. ***Papillaria crocea***, a winter survivor in NZ. Photo by Janice Glime.

Figure 8. ***Hypopterygium didictyon***, a genus that can withstand temperatures to -3°C. Photo by Juan Larrain, with permission.

Figure 9. ***Rhizogonium novae-hollandiae***. ***Rhizogonium bifarium*** survives temperatures as low as -3°C in New Zealand. Photo by Niels Klazenga, with permission.

Figure 10. ***Cyathophorum bulbosum*** from Tasmania, a moss that survives freezing. Photo by Vita Plasek, with permission.

Figure 11. ***Gigaspermum repens*** with capsules, a moss that tolerates freezing in Australia. Photo by David Tng, with permission.

Figure 12. ***Goniomitrium acuminatum*** subsp. ***enerve*** with capsules, a moss that tolerates freezing in Australia. Photo by David Tng, with permission.

Figure 13. ***Rhizogonium spiniforme*** with capsule, a moss that tolerates frost. Photo by Janice Glime.

Figure 14. ***Takakia lepidozioides*** in its native habitat in Japan. This moss species remains healthy through the Hokkaido winters. Photo from the Digital Herbarium of the University of Hiroshima, with permission.

Figure 15. ***Takakia lepidozioides***, a winter survivor. Photo from the Digital Herbarium of University of Hiroshima, with permission.

Figure 16. ***Sphagnum cristatum***, a New Zealand species that survives in winter there. Photo by Janice Glime.

Figure 17. ***Plagiomnium novae-zealandiae*** from New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 18. ***Haplomitrium hookeri***, a liverwort that is sensitive to freezing in the lab but survives it in the field. Photo by Des Callaghan, with permission.

Figure 19. ***Haplomitrium mnioides***, a liverwort that is sensitive to freezing in the lab but survives it in the field. Photo by Li Zhang, with permission.

Experiences with freezing in ***Plagiomnium undulatum*** (Figure 20) may help us to understand some of these differential responses (Hudson & Brustkern 1965). If this moss is cooled slowly, it experiences extracellular freezing; this prevents the intracellular freezing that could be fatal. Following that experience, the leaves can be cooled down to -30°C without injury. The slow freezing prevents the formation of extensive extracellular ice. Young shoots, however, cannot withstand temperatures below -12°C.

Figure 20. ***Plagiomnium undulatum***, a moss that uses extracellular freezing to prevent intracellular crystal formation. Photo by Michael Lüth, with permission.

Among the thallose liverworts, ***Lunularia*** (Figure 21), ***Pellia*** (Figure 22), ***Preissia*** (Figure 23-Figure 24), ***Riccardia*** (Figure 25), ***Riccia*** (Figure 26), and ***Marchantia polymorpha*** (Figure 27), all survive frost (Fletcher 1982) and remain healthy. On the other hand, the thallose liverworts ***Moerckia blyttii*** (Figure 28-Figure 29), ***Symphogyna*** sp. (Figure 30), ***Corsinia coreandra*** (Figure 31-Figure 32), and ***Asterella*** (Figure 33) all can become severely bleached when subjected to frost. ***Dumortiera hirsuta*** (Figure 34-Figure 35) doesn't die, but it becomes blackened. Similarly, ***Fossombronia*** (Figure 36) and **Anthocerotophyta** experience decay, but for them the decay is a normal winter occurrence; growth resumes in the spring. In the greenhouse, which reaches -5.5°C, ***Asterella*** and ***Monoclea forsteri*** (Figure 37) are blackened by frost, whereas ***Marchantia*** spp, ***Dumortiera hirsuta***, ***Anthoceros punctatus*** (Figure 38), and ***Phaeoceros laevis*** (Figure 39) remain healthy in the same greenhouse.

Figure 21. ***Lunularia cruciata***, a frost-tolerant thallose liverwort. Photo from <www.aphotofauna.com>, with permission.

Figure 22. ***Pellia endiviifolia*** males with reddish antheridial cavities & females in center, a species that survives freezing. Photo by David Holyoak, with permission.

Figure 23. ***Preissia quadrata*** with archegoniophore, member of a genus that survives freezing. Photo by Michael Lüth, with permission.

Figure 24. ***Preissia quadrata*** thallus section showing several globose oil bodies that may help it to survive desiccation and freezing. Photo by Kristian Peters, with permission.

Figure 25. ***Riccardia*** sp, a thallus that survives freezing. Photo by Niels Klazenga, with permission.

Figure 26. ***Riccia beyrichiana***, a genus that is able to survive frost – and desiccation. Photo by Jan-Peter Frahm, with permission.

Figure 27. ***Marchantia polymorpha*** with gemmae cups, a species that survives frost. Photo by Michael Lüth, with permission.

Figure 28. ***Moerckia blyttii***, a liverwort that is sensitive to frost, becoming bleached. Photo by Michael Lüth, with permission.

Figure 29. ***Moerckia blyttii*** habitat. Photo by Michael Lüth, with permission.

Figure 30. ***Symphyogyna podophylla***, a liverwort genus in which one species is sensitive to frost and becomes bleached. Photo by Andras Keszei, with permission.

Figure 31. ***Corsinia coriandrina***, a thallose liverwort that is sensitive to frost under some conditions. Note bleached tissues, especially in the bottom center. Photo by Michael Lüth, with permission.

Figure 32. ***Corsinia coriandrina*** in its habitat on a ledge, a thallose liverwort that is sensitive to frost under some conditions. Photo by Michael Lüth, with permission.

Figure 33. ***Asterella lindenbergiana***, a thallose liverwort that is sensitive to frost. Photo by Michael Lüth, with permission.

Figure 34. ***Dumortiera hirsuta***, a thallose liverwort that is sensitive to frost and becomes blackened, but doesn't die. Photo by Michael Lüth, with permission.

Figure 35. ***Dumortiera hirsuta*** habitat. Photo by Michael Lüth, with permission.

Figure 36. ***Fossombronia angustata***, a species in which frost causes decay, a normal winter occurrence. Note the patches of colorless plants. Photo by Michael Lüth, with permission.

Figure 37. ***Monoclea forsteri***, a species that is blackened by frost. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Anthoceros punctatus***, a species that survives to -5.5°C. Photo by Jonathan Sleath, with permission.

Figure 39. ***Phaeoceros laevis*** with capsules, a species that remains healthy to -5.5°C. Photo by Michael Lüth, with permission.

Corsinia coreandra (Figure 31-Figure 32) is a puzzle. It is a xerophyte, but in cultivation frost causes it to become bleached (Fletcher 1982). At the same time in the same garden as the cultivation containers, it remains healthy on an exposed wall top and likewise remains healthy in the greenhouse that goes down to -5.5°C.

Much of what we know about cold tolerance has come from Antarctic studies. The Antarctic continent has only

2% of its land free from ice (Seppelt & Ochyra 2008). These areas are dominated by bryophytes (24 species of mosses; 1 liverwort), lichens, and algae.

We have learned that macromolecular substances (ice-active substances or IASs) can modify the shape of the growing ice crystals (Raymond & Fritsen 2001). These semipurified substances from ***Bryum*** sp. (Figure 40) from the Antarctic contain both protein and carbohydrate. The substances lose most of their recrystallization ability by heat treatment. Raymond and Fritsen suggest that these substances might increase freezing tolerance by preventing ice recrystallization.

Figure 40. ***Bryum pseudotriquetrum*** in Antarctica, a species in which protein and carbohydrate might increase freezing tolerance by preventing ice recrystallization. Photo by Catherine Beard, with permission.

Some bryophytes thrive in habitats where they regularly get exposed to sub-zero temperatures. ***Bryoxiphium norvegicum*** (Figure 41) is such a species (Shirasaki 1984). In Japan, ***B. norvegicum*** subsp. ***japonicum*** lives in an altitudinal range of 80-2350 m, being most abundant in districts where deep snow covers the ground for a long period. But it does not grow where the snow is, but rather grows on the vertical sides of overhanging rocks in ravines. Hence, it survives winter without the protection of snow, but it is sheltered by the rocks from the cold, desiccating winds.

Figure 41. ***Bryoxiphium norvegicum***, a species that grows on vertical surfaces where it is exposed to sub-zero temperatures without snow cover in winter. Photo by Bob Klips, with permission.

Ice Crystals

Ice crystals can cause plant tissues to dry out. Ice crystals are very hygroscopic and thus their presence can result in water being drawn out of tissues. But they also gather water from the atmosphere. Moffett *et al*. (2009) suggest that these ice crystals can sequester water that becomes available when they melt. Because bryophytes are able to absorb water through their leaves, this water can be immediately available and provide rapid rehydration.

Rod Seppelt (pers. comm. 7 April 2015) does not consider it to be unusual that ***Ricciocarpos natans*** (Figure 2-Figure 4) and ***Riccia fluitans*** (Figure 5) can be encased in ice or survive under a layer of snow. As he points out, temperatures within the ice are not typically very cold. As an example, he cites putting a pot of water 80 cm under the Alaskan snow overnight. The air temperature that night dipped to -22°C, but the pot of water remained unfrozen.

Of course dehydration caused by freezing can have other consequences. Dependence on the symbiont ***Nostoc*** is interrupted and nitrogen fixation is significantly reduced in winter due to dehydration resulting from freezing in the epiphytic leafy liverwort ***Porella*** (Figure 42-Figure 43) in Oregon, USA (De Gezelle 2003).

Figure 42. ***Porella cordeana*** in one of its vertical habitats where the symbiotic Cyanobacterium ***Nostoc*** provides it with needed nitrogen. Photo by Michael Lüth, with permission.

Figure 43. ***Porella cordeana*** on a vertical substrate, a species that suffers in winter from diminished nitrogen fixation by its symbiont. Photo by Michael Lüth, with permission.

Desiccating Conditions

If you have ever gone out in early spring in areas where there is snow cover all winter, bryophytes provide a refreshing green cover on the newly emergent ground. This fresh green color requires the presence of water to rehydrate the tissues. But where does it come from?

In many temperate regions, spring brings rain, hence making rehydration an easy task. But in some regions, my own home in the Keweenaw Peninsula of Michigan included, snowmelt is followed by drought, and this is exacerbated along roads by the sand and salt that was used to provide traction for vehicles during winter ice and snow.

Nevertheless, in northern habitats, snowmelt can provide water for a considerable time. In the Cairngorm Mountains, Scotland, ***Kiaeria starkei*** (Figure 44) is immediately ready for photosynthetic activity when its own snow cover disappears (Woolgrove & Woodin 1996). It has just spent its winter at temperatures of 0°C to slightly above, but with no light penetration while the snow depth is greater than 50 cm. When the snow disappears from it, its tissue chlorophyll recovers rapidly to 250% of its winter low and within two weeks its carbohydrate concentrations increase by 60%. This moss has nitrate reductase activity and is able to take advantage of pollutant nitrate, accumulated by the snow, that becomes available as the snow melts.

Figure 44. ***Kiaeria starkei***, a species that is ready to photosynthesize as it emerges from the snow. Photo by Michael Lüth, with permission.

One advantage for bryophytes is that they have a low temperature compensation point. Hence, snowbed bryophytes such as ***Anthelia juratzkana*** (Figure 45-Figure 47) and ***Polytrichastrum sexangulare*** (Figure 48-Figure 49) can maintain photosynthesis at low temperatures with a lower temperature compensation point of about -4 to -5°C. Furthermore, ***A. juratzkana*** can survive in the dark under cold, wet conditions for nine months with no effect on its photosynthetic capability. This makes ***A. juratzkana*** well adapted to grow in the border zone along permanent snow patches. However, the net photosynthesis is reduced due to an increase in respiration rate. ***Polytrichastrum sexangulare***, on the other hand, does not tolerate this border regime as well as does ***A. juratzkana***.

Figure 45. ***Anthelia juratzkana*** growing in a late snowbed area. Photo by Michael Lüth.

Figure 46. ***Anthelia juratzkana*** showing dense alpine growth. Photo by Michael Lüth, with permission.

Figure 47. Close view of the leafy liverwort ***Anthelia juratzkana***. Photo by Michael Lüth, with permission.

Figure 48. ***Polytrichastrum sexangulare*** at alpine lake in Europe. Photo by Michael Lüth, with permission.

Figure 49. ***Polytrichastrum sexangulare*** with water drops. This species does not tolerate cold, dark storage in wet conditions as well as ***Anthelia juratzkana*** is able to do. Photo by Michael Lüth, with permission.

In tracheophytes, freezing can cause ice to form within cells, potentially causing membrane damage and subsequent loss of cell constituents. Lenne *et al*. (2010) write "A dehydrating moss gathers no ice." Using the widespread moss ***Ceratodon purpureus*** (Figure 50-Figure 51), they demonstrated that no ice accumulates in the cells during freezing. But external ice does induce desiccation. The effects of this desiccation depend on the cell type. Water-filled hydroid cells **cavitate** like tracheophyte xylem cells, becoming **embolized** (blocked, in this case by ice) at -4°C. Parenchyma cells of the inner cortex of the stem exhibit **cytorrhysis** (complete and irreversible collapse of a plant cell wall due to loss of water through osmosis), losing 20% of their original volume at -20°C **nadir temperature** (lowest temperature of a cycle). It is puzzling that chlorophyll fluorescence shows no evidence of damage after thawing from a -20°C event, especially since the sugar concentrations are insufficient to confer freeze tolerance in these conditions (see below). Furthermore, ice nucleation occurs in hydrated tissues at ~-12°C. The answer to this puzzle seems to lie in the desiccation itself. No damage occurs to those desiccated mosses at -20°C. The very desiccating nature of ice crystals appears to be the mechanism that prepares the moss for the low temperatures.

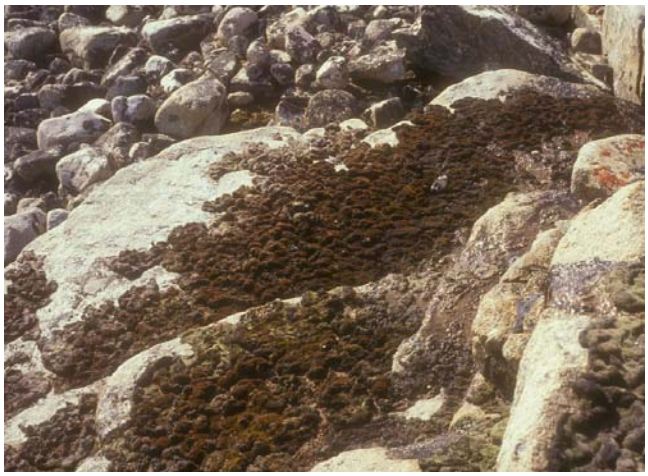

Figure 50. ***Ceratodon purpureus*** in Antarctica, a species with small leaf cells that do not accumulate ice crystals in winter. Photo courtesy of Rod Seppelt.

Figure 51. ***Ceratodon purpureus*** with capsules, a species that gathers no internal ice. Photo by Ivanov, with permission.

This desiccation relationship is supported in the Antarctic moss ***Polytrichum juniperinum*** (Figure 52) wherein repeated freeze-thaw cycles cause a greater reduction in photosynthesis than constant freezing for the same time period (Kennedy 1993). This is much like the effect of repeated dehydration/rehydration that causes a net carbon loss. This is supported by the observation that freeze-thaw cycles every 12 hours cause more damage than those every 24 or 48 hours. Most of the damage occurs during the first cycle with little occurring during subsequent cycles. Kennedy found that at 10°C the gross CO_2 flux is directly proportional to moss water content between 0.3 and 3.5 g g^{-1} dry mass. Mosses with a low water content withstand freeze-thaw cycles to sub-zero temperatures better than do samples with a high water content. Kennedy suggests that on Signy Island in the Antarctic the populations of ***Polytrichum juniperinum*** may be limited in distribution by sub-zero temperatures and freeze-thaw cycles at times when snow cover is insufficient to provide insulation.

Figure 52. ***Polytrichum juniperinum***, a moss that is damaged by freeze-thaw cycles when snow cover does not provide insulation. Photo by Jan-Peter Frahm, with permission.

Davey (1997) examined Antarctic bryophytes and demonstrated the importance of water. The photosynthetic rate decreased as the length of the dehydration period increased in all bryophytes examined. The photosynthetic capacity is affected by stress, and Davey found that both desiccation and winter freezing caused a loss of photosynthetic capacity. But the base level of photosynthetic capacity is able to survive both. Furthermore, frequent dehydration and rehydration cycles cause a loss of photosynthetic rate that is greater than that in continuous dehydration. Davey hypothesized that water availability is an important contributor to the distribution of bryophytes in the Antarctic, where winter-like weather can occur on almost any day of the year.

Barker *et al*. (2005) found bleaching in ***Syntrichia caninervis*** (Figure 53) during winter in the Mojave Desert, USA. They attributed this loss of green color to frequent rain events during warmer months that year, citing appearance of chlorosis just after that. This is consistent with the effects of frequent dehydration-rehydration events seen by Davey (1997). Under this regime, particularly for short, light rainfall events, the plants do not have enough time to repair membranes before they become dehydrated again, thus losing energy with each mild rainfall event. This leaves them with diminished color for the winter, a condition hopefully to be repaired in the spring.

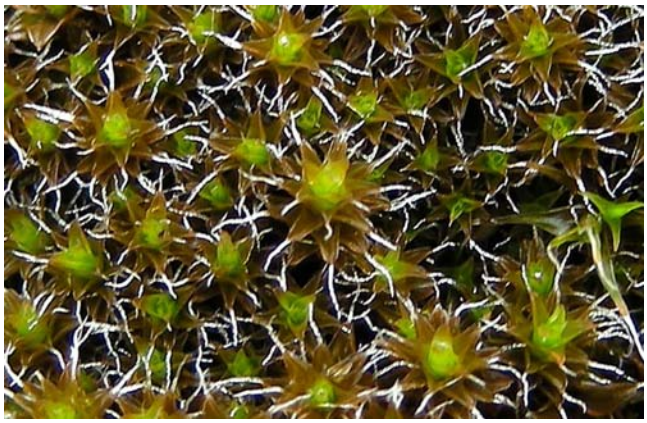

Figure 53. ***Syntrichia caninervis***, a desert species that suffers from too much rain in winter by losing its green color. Photo by Michael Lüth, with permission.

Crossidium crassinervium (Figure 54), from the Mojave Desert, benefits from late winter rain because it permits the moss to dry slowly (several days), whereas in summer the moss dries in as little as 3 hours (Stark 2005). The winter months of October to April constitute the hydrated period for this species, with hydration periods lasting 3.7-4.9 days.

Figure 54. ***Crossidium crassinervium***, a moss that benefits from late winter rains in the desert. Photo by Michael Lüth, with permission.

Desiccation Tolerance

Desiccation tolerance is seasonal, probably in most bryophytes. Only the moss ***Andreaea rothii*** (Figure 55-Figure 56) failed to show seasonal variation in net assimilation following 24 hours of remoistening, compared to clear seasonal differences in the leafy liverwort ***Plagiochila spinulosa*** (Figure 57-Figure 58) and mosses ***Hylocomium splendens*** (Figure 59), ***Scorpiurium circinatum*** (Figure 60), ***Syntrichia ruralis*** (Figure 61-Figure 62), and ***Racomitrium aquaticum*** (Figure 63-Figure 64) (Dilks & Proctor 1976). Those with seasonal variation usually had low desiccation tolerance in autumn and winter and greater tolerance in spring and summer. ***Hylocomium splendens*** differed in having relatively high tolerance in January (winter), with little change from then until July.

Figure 55. ***Andreaea rothii***, a species that shows no seasonal variation in its net assimilation following 24 hours of hydration. Photo by Michael Lüth, with permission.

Figure 56. ***Andreaea rothii*** in a typical vertical rock habitat where snow does not accumulate. Photo by Michael Lüth, with permission.

Figure 57. ***Plagiochila spinulosa*** in a soil bank habitat where it exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 58. ***Plagiochila spinulosa***, a leafy liverwort that has seasonal differences in its hydrated photosynthetic rate. Photo by Michael Lüth, with permission.

Figure 59. ***Hylocomium splendens*** with clinging snow, a moss that exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 60. ***Scorpiurium cirrcinatum***, a moss that exhibits seasonal differences in photosynthesis. Photo by Michael Lüth, with permission.

Figure 61. ***Syntrichia ruralis*** habitat in a cliff splash zone. Photo courtesy of Betsy St Pierre.

Figure 62. ***Syntrichia ruralis***, a species that shows seasonal differences in photosynthetic rates. Photo by Michael Lüth, with permission.

Figure 63. ***Racomitrium aquaticum***, a species that has more desiccation tolerance in spring and summer than in other seasons and has seasonal photosynthetic differences. Photo by Aimon Niklasson, with permission.

Figure 64. ***Racomitrium aquaticum*** in one of its habitats. Photo by Michael Lüth, with permission.

Burch (2003) noted that some mosses are able to survive **cryopreservation** (preservation at low temperatures) with no prior treatment. She suggested that their natural desiccation tolerance already gave them adequate protection during cryopreservation. What is it about freezing that actually kills or damages the bryophytes? Crystals can damage the membranes, but isn't the real damage ultimately desiccation damage? For example, 90-100% of the protonemata of the desiccation-tolerant ***Bryum rubens*** (Figure 65) survived freezing, whereas only 30% of those encapsulated and 20% non-encapsulated ***Ditrichum cornubicum*** (Figure 66) protonemata, with limited desiccation tolerance, survived freezing. These two species each had slightly better survival numbers after 18 days of desiccation with no freezing. ***Cyclodictyon laete-virens*** (Figure 67), a desiccation-intolerant species, did not survive desiccation or freezing. In ***D. cornubicum***, pretreatment with sucrose or ABA in the medium caused a reduction in growth rate of the protonemata, but these compounds resulted in a high level of protection against tissue damage in both dehydration and freezing – 100% regeneration of pretreated plants after thawing compared to 53% of controls (Burch & Wilkinson 2002). Sucrose plus ABA gave the best results.

Figure 65. ***Bryum rubens***, a moss whose protonemata are desiccation-tolerant and survive freezing. Photo by Des Callaghan, with permission.

Figure 66. ***Ditrichum cornubicum***, a moss whose protonemata have limited desiccation tolerance and low freezing survival. Photo by David T. Holyoak, with permission.

Figure 67. ***Cyclodictyon laete-virens***, a moss that does not survive desiccation or freezing. Photo by Des Callaghan, with permission.

Syntrichia ruralis (Figure 62) is one of the model organisms for studying desiccation tolerance. When subject to slow freezing at 3°C decrease in temperature per hour to -30°C, hydrated ***Syntrichia ruralis*** suffers only temporary metabolic changes, and these are reversible (Malek & Bewley 1978). Malek and Bewley attributed the changes to desiccation tolerance resulting from extracellular ice formation. When this same moss is subject to rapid freezing in liquid nitrogen and rapid thawing in 20°C water, all aspects of its metabolism deteriorate. Ribosomes, proteins, and ATP levels decrease and protein synthesis activity is rapidly lost. Malek and Bewley suggest that these problems are the result of intracellular ice crystals. Changing the freezing rate to 60°C per hour – a slower rate than in liquid N, but still a rapid rate – only reduces the levels of ATP and protein synthesis. The **polyribosomes** (protein-synthesizing apparatus) remain intact and active 24 hours after the freeze-thaw cycle. Segreto *et al*. (2010) reported that all species cryopreserved *in situ* regenerated mostly through budding; the number of regenerating samples correlates positively to desiccation tolerance and show higher frost tolerance than previously thought. Herbarium samples up to 7 years old of the most desiccation-tolerant species regenerate by protonemata; shoot tips regenerate better than small plant fragments.

Desiccation tolerance can be an **antagonistic** (one species benefits at the expense of another) interaction. ***Sphagnum fuscum*** (Figure 68) and ***Dicranum elongatum*** (Figure 69) dominate a subarctic mire (Sonesson *et al*. 2002). In winter, ***Sphagnum fuscum*** growth increased when ***Dicranum elongatum*** was its immediate neighbor, but ***D. elongatum*** grew better when it grew with other members of its own species. Neither increased temperature nor UV-B radiation affected these relationships, implying that moisture relations were probably important.

Ice-nucleating Proteins

Ice-nucleating proteins can help to create desiccating conditions and prevent cell freezing. These proteins are small structures that become surrounded by ice, but the water does not crystallize. The principle has been used by orange growers to prevent desiccation of the fruits during winter freezing events. Small nucleating bacteria are able to accomplish desiccation protection by out-competing the larger nucleating bacteria. These small species are sprayed on oranges to protect them. Such proteins or bacteria form centers for ice formation on the outsides of cells, providing a protective covering (Zachariassen & Kristiansen 2000).

Figure 68. ***Sphagnum fuscum***, a species that benefits from having ***Dicranum elongatum*** as its neighbors. Photo by Michael Lüth, with permission.

Figure 69. ***Dicranum elongatum***, a mire species that benefits from association with its own species more than by associating with ***Sphagnum fuscum***. Photo by Michael Lüth, with permission.

Clouds use nucleation centers to create their precipitation (Ahern *et al*. 2007). Bacteria have been known from clouds for a long time. Clouds may be an ideal habitat for these bacteria to live and thrive. Ahern and coworkers found 100 **OTUs** (operational taxonomic units – used when species cannot be named) among 256 clones from clouds. Half of these were identified as bacteria from **psychrophilic** terrestrial habitats (habitats where low-temperature-tolerant organisms can live). Among these bacteria, a mix of fluorescent *Pseudomonas* species dominate and some are known ice nucleators. But none of the cultures demonstrated the ice-nucleation gene. Rather, 55% of the isolates from cloud and rain samples had significant biosurfactant activity. **Surfactants** influence droplet size and are important in lowering the critical supersaturations necessary for activating aerosols into cloud condensation nuclei. Such bacteria facilitate water scavenging and counteract desiccation. Could they perform such functions in some bryophytes?

In ***Sphagnum capillifolium*** (Figure 70-Figure 71) the **chlorophyllous** (containing chlorophyll) cells exhibit extended freezing **cytorrhysis** immediately after ice nucleation at -1.1°C in water (Buchner & Neuner 2010). This cytorrhysis is exhibited as cell shrinkage that appears within only 2 seconds. And the shrinkage is significant – 82%, with chloroplast diameter reduction from 8.9 to 3.8 μm. This is accompanied by a sudden rise in chlorophyll fluorescence. On the other hand, frost damage occurs at a much lower temperature (LT50 at -16.1°C) (LT50 = median time until death after exposure of organism to toxic substance or stressful condition). The ice-nucleation temperature of -1.1°C is likewise the temperature threshold of PS II. Surprisingly, the LT50 for freezing in ***S. capillifolium*** is higher than that in most tracheophytes in the European Alps in the summer.

Atmospheric Source

One big question in this story is the source of the nucleating proteins. Until recently, bacteria seemed to be the only organic source of nucleating proteins (Möhler *et al*. 2008). But only a few bacteria, the pseudomonads, seem capable of this role (Lindow 1983; Ahern *et al*. 2007). This notion has been challenged by the research of Kieft and coworkers (Kieft 1988; Kieft & Ahmadjian 1989; Kieft & Ruscetti 1990) and more recently by Moffett *et al*. (2009).

Bauer *et al*. (2002) supported their challenge and reported that both bacteria and fungal spores contribute to the organic content of cloud water. In fact, the fungal spores in clouds of the Austrian Alps contribute 1.5% of the organic content, whereas the bacteria contribute only 0.01%. Although Pouleur and coworkers did not discuss the roles of these groups in nucleation, their study (Pouleur *et al*. 1992) suggests that slime molds might also provide nucleating proteins.

Hyphomycetous fungi (***Fusarium*** spp.; Figure 72) were also added to the list of organisms providing nucleating proteins to clouds (Pouleur *et al*. 1992). We also know that the fungal partner of at least some lichens contribute nucleating proteins (Kieft 1988; Kieft & Ahmadjian 1989; Kieft & Ruscetti 1990) and that the ***Fusarium*** proteins are more similar to those of lichens than to those of bacteria (Pouleur *et al*. 1992).

Figure 70. ***Sphagnum capillifolium***, a species that loses chlorophyll in response to chilling. Photo by Michael Lüth, with permission.

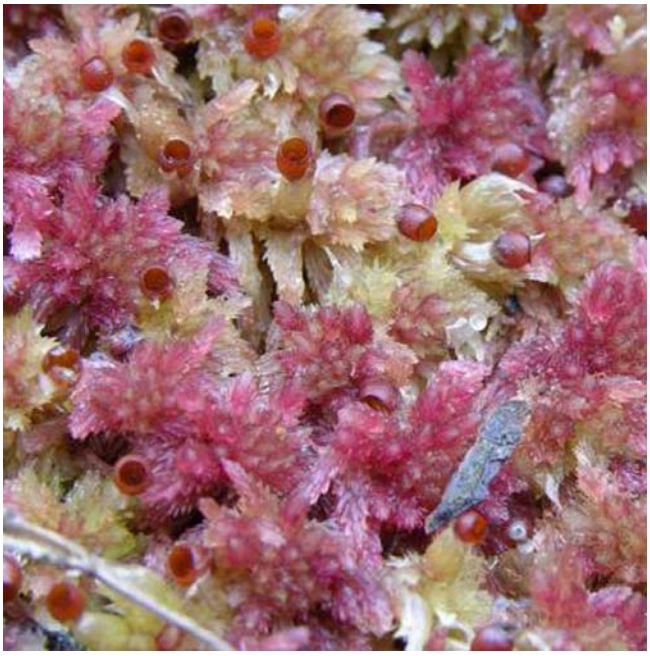

Figure 71. ***Sphagnum capillifolium*** in Chile, showing plants with diminished chlorophyll. Photo by Juan Larrain, with permission.

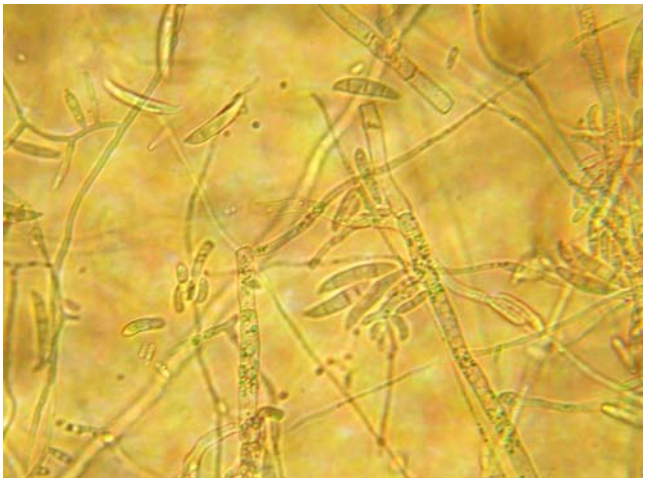

Figure 72. ***Fusarium*** with macroconidia, a filamentous fungal genus that serves as an ice-nucleating center. Photo by Ninjatacoshell, through Creative Commons.

Despres *et al*. (2007) determined aerosol particles in the air by using DNA sequencing. They found that most of the bacteria were **Proteobacteria**, with some **Actinobacteria** and **Firmicutes**. Fungal DNA came from **Ascomycota** and **Basidiomycota**, most likely from spores. Two different DNA sequences came from moss spores.

Christner *et al*. (2008) reported that ice nucleators are widespread in snowfall and the most active ones are biological. Most of these are bacteria. Many of these nucleators, therefore, are likely to be added to the mosses during snowfall and may contribute their survival of low temperatures and winter desiccation.

Fukuta (1966) found that more than 20 organic compounds out of 329 were able to nucleate ice at temperatures >-5°C. Hence, it is possible that even pollutants may contribute to nucleation of water on bryophytes.

Nucleating Proteins in Lichens

Our knowledge of lichens may help us to understand the nucleation relationship in bryophytes. Like bryophytes, lichens are able to survive year round and renew their photosynthetic activity when suitable temperatures and hydration resume. Perhaps the response of lichens can give us some insight into moss behavior relative to nucleation. Most of the **epilithic** (rock-dwelling) lichens (*Rhizoplaca*, *Xanthoparmelia*, and *Xanthoria*) tested by Kieft (1988) had ice nucleation at temperatures above -8°C, whereas their substrates showed negligible nucleation above that temperature. The nucleation activity in the lichen appears to be non-biological. No nucleation-active bacteria could be isolated, and the activity did not cease when the lichen was heated to 70°C or subjected to sonication. An axenic culture of the fungal part of the lichen *Rhizoplaca chrysoleuca* showed nucleation activity at -1.9°C. Kieft hypothesized that these frost-tolerant lichens benefit from increased moisture deposition that results from ice nucleation.

Henderson-Begg *et al*. (2009) remind us that for water to freeze above -36.5°C requires the activity of an ice nucleator. Bacteria are the best known of these, inducing freezing at temperatures up to -1.8°C, but seem to be of little importance in the lichens. The nucleators are common in lichens and can become airborne. Many of these are non-bacterial, but are biological, probably fungal and lichen.

There are several studies that support the presence of lichen fragments in the atmosphere (Tormo *et al*. 2001; Ahern *et al*. 2007). Marshall (1996) demonstrated that lichen **soredia** (asexual reproductive structures) were the most abundant of the airborne propagules of lichens, with peaks occurring after the winter snowmelt while subzero temperatures continued.

Kieft and Ahmadjian (1989) found that of 14 species of **mycobionts** (fungal partners) in lichens, five have nuclei active at -5°C. However none of the 13 photobionts (algae & Cyanobacteria) have ice-nucleating activity at -5°C or warmer. Hence, the ice-nucleating nuclei are produced by the fungal partner of the lichen. Kieft and Ahmadjian suggested that these ice-nucleating proteins are involved in moisture uptake and frost protection.

Kieft and Ruscetti (1990) found that biological ice nuclei in the lichen *Rhizoplaca chrysoleuca* were active at ~-4°C. Their sensitivity to various substances indicated that they were proteinaceous, and they were relatively heat stable and active without lipids, demonstrating that they were significantly different from bacterial ice nuclei.

Nucleating Proteins as a Source of Water

Lindow (1983) found that ice-nucleation activity occurs primarily in the outer membrane of the cells of *Pseudomonas syringae* and *Escherichia coli* into which it has been inserted.. It does not occur in soluble components of these cells. The ability of the ice-nucleating bacteria to operate depends on incubation temperature, growth medium composition, culture age, and genotype (Lindow *et al.* 1982). Their optimum conditions for nucleation in culture occur on nutrient agar containing glycerol at 20-24°C. Their ability to mitigate ice injury on corn seedlings depends on the bacterial population size and the number of ice nuclei active at that temperature.

Compounds for Winter?

Bryophytes produce record numbers of secondary compounds. These are best known for their antibiotic effects, but they can also play a role in both drought tolerance and freezing survival (Xie & Lou 2009). Among these, **bibenzyls** and **bis(bibenzyls)** have desiccation tolerance activity; **phenylpropanoids** have freeze tolerance activity. But the nature of these activities is unknown.

We know from several studies that the proportions of various fatty acids change with temperature (Saruwatari *et al*. 1999). Among these, linolenic acid and eicosapentaenoic acid might increase freezing-tolerance, as suggested by ***Marchantia polymorpha*** (Figure 27). Xie and Lou (2009) likewise reported the freeze tolerance activity of fatty acid derivatives in bryophytes.

Sugars

Sugar concentrations have a role in frost tolerance. **Sucrose** can increase the ability of bryophytes to tolerate rapid drying (Stark & Brinda 2015). Among the bryophytes tested by Rütten and Santarius (1992), only ***Mnium hornum*** (Figure 73-Figure 74) among seven **Bryidae** and one of **Marchantiidae** lack an increase in sucrose concentration concomitant with an increase in frost hardiness. Insignificant changes in **glucose** and **fructose** contents accompany these frost hardiness events.

Figure 73. ***Mnium hornum*** forest floor habitat. Photo by Michael Lüth, with permission.

Brachythecium rutabulum (Figure 75-Figure 76) and ***Hypnum cupressiforme*** (Figure 77-Figure 78) have high sucrose concentrations in summer, similar to those of other species in winter, and thus are frost tolerant even in summer (Stark & Brinda 2015). Those mosses that are highly frost-resistant have a total sugar concentration of ~90-140 mM. Of this sugar, 80-90% is sucrose. Artificial degradation of the sucrose during higher temperatures causes a decline in cold hardiness, supporting the hypothesis that it is important in frost hardiness in these species.

Figure 74. ***Mnium hornum***, a moss that does not contain more sugar with its frost hardiness. Photo by Michael Lüth, with permission.

Figure 75. ***Brachythecium rutabulum*** forest floor habitat in England. Photo by Janice Glime.

Figure 76. ***Brachythecium rutabulum***, a species with high sucrose content and high frost tolerance, even in summer. Photo by Michael Lüth, with permission.

Figure 77. ***Hypnum cupressiforme*** in one of its many habitats. Photo by Dick Haaksma, with permission.

Figure 78. ***Hypnum cupressiforme***, a species with high sucrose content and high frost tolerance, even in summer. Photo by Michael Lüth, with permission.

Some species [***Polytrichastrum formosum*** (Figure 79-Figure 81), ***Atrichum undulatum*** (Figure 82), ***Plagiomnium affine*** (Figure 83-Figure 84), ***Mnium hornum*** (Figure 73-Figure 74), ***Pellia epiphylla*** (Figure 85-Figure 86)] exhibit a distinct increase in cold tolerance from summer to winter (Rütten & Santarius 1992). Mosses have significant differences in frost resistance between summer and winter (15->25°C), but the thallose liverwort ***Pellia epiphylla*** experiences relatively little winter hardening capacity.

Figure 79. ***Polytrichastrum formosum*** on the forest floor in Europe. Photo by Michael Lüth, with permission.

Figure 80. ***Polytrichastrum formosum*** with frost, a species that has a distinct increase in cold tolerance from summer to winter. Photo by Aimon Niklasson, with permission.

Figure 81. ***Polytrichastrum formosum*** leaf lamellae. The role of lamellae in frost protection is unknown. Photo by Michael Lüth, with permission.

Figure 82. ***Atrichum undulatum***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by David T. Holyoak, with permission.

Figure 83. ***Plagiomnium affine*** forest floor habitat. Photo by Michael Lüth, with permission.

Figure 84. ***Plagiomnium affine***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by Janice Glime.

Figure 85. ***Pellia epiphylla*** protected habitat under grass bank of flush in Wales. Photo by Janice Glime.

Figure 86. ***Pellia epiphylla***, a species that has a distinct increase in cold tolerance from summer to winter. Photo by David T. Holyoak, with permission.

Melick and Seppelt (1994) suggest that the lack of significant changes in soluble carbohydrates in Antarctic bryophytes may result from the extreme climate and the rapid temperature fluctuations during the growing season. On the other hand, maximum water content is present in the summer. Chlorophyll levels decrease in winter in both total chlorophyll and the chlorophyll *a*:*b* ratio, as do the total carotenoids. This decrease may be a response to low light levels that are insufficient for making more pigment.

Using the ***Physcomitrella patens*** (Figure 87) protonema as a model organism, Nagao *et al*. (2003, 2005) concluded that ABA-induced soluble sugars play a role in freezing tolerance. The accumulation of the sugars, at the expense of starches, is associated with morphological changes in the organelles and reduce freezing-induced structural damage to the plasma membrane, while the freezing tolerance of the protonemal cells increases. Nagao *et al.* (2006) identified the sugar as **theanderose**, a sucrose that occurs in close association with ABA treatment that enhances freezing tolerance. Cycloheximide inhibits the accumulation of theanderose, resulting in a marked decrease in freezing tolerance. The accumulation of theanderose is promoted during cold acclimation and treatment with hyperosmotic solutes, both of which increase cellular freezing tolerance.

Figure 87. ***Physcomitrella patens***, a moss that stores the sugar **theanderose** in preparation for winter. Photo by Michael Lüth, with permission.

Using the bryological lab rat ***Physcomitrella patens*** (Figure 87), Oldenhof *et al*. (2006) demonstrated that sucrose helps to protect cells during freezing and drying, but accumulation of sucrose alone is not sufficient for survival. ABA serves to cause this sucrose accumulation, up to 22% of dry weight, but only 3.7% occurs in non-ABA-treated tissues. A combination of ABA treatment and the cryoprotectant DMSO permit the tissues to survive a freeze-thaw cycle down to -80°C. DMSO-mediated changes involved in the membranes are important and may be relevant to the essential desiccation tolerance.

Polyols may contribute to cold hardiness as well. Tearle (1987) found that Antarctic lichens contained up to three times the amount of polyols when compared to temperate lichens, endowing them with extra freezing protection. The soluble sugars and polyols from mosses and lichens leach into the fellfield soils in the spring.

ABA

ABA is the stress hormone, and it plays a role in freezing tolerance of plants as well (Minami *et al*. 2003; Takezawa *et al*. 2011). Nevertheless, slow freezing of the protonemata of ***Physcomitrella patens*** to -4°C under normal growth conditions kills more than 90% of the cells. Application of ABA for 24 hours causes a marked increase in the freezing tolerance (see also Nagao *et al*. 2001, 2005, 2006). Cold treatment only slightly increases the freezing tolerance within the same period. Treatment with ABA causes a marked increase in expression of all the PPAR genes within 24 hours. Several of these genes also respond to cold, but much more slowly than they respond to ABA. Treatment with hyper-osmotic concentrations of NaCl and mannitol also increases the expression levels of eleven PPAR genes and the freezing tolerance of the protonemata. Minami and coworkers (2003) suggest that these relationships indicate that stresses increase the expression of genes that result in protection of the protonemata, but the nature of that relationship is unclear.

Nevertheless, in ***Physcomitrella patens*** (Figure 87) protonemata, as in tracheophytes, freezing tolerance increases following incubation at low temperatures in the range of 0-10°C, indicating the importance of acclimation (Minami *et al.* 2005). This tolerance is accompanied by an accumulation of several transcripts for **late-embryogenesis-abundant (LEA)** proteins and boiling-soluble proteins. De-acclimation causes reduction in expression of these proteins and loss of freezing tolerance. But surprisingly, unlike events in tracheophytes, in ***P. patens*** low-temperature-induced freezing tolerance does not coincide with an increase in endogenous ABA, despite increases in expression of stress-related genes. In short, the acclimation is somewhat different from that of tracheophytes.

These observations are further confounded by the experiments of Minami *et al*. (2003) on ***Physcomitrella patens*** (Figure 87). They found that treatment with ABA for 24 hours greatly increases the freezing tolerance of the protonemata; cold treatment alone has only a slight effect on freezing tolerance. Even slow freezing to -4°C kills more than 90% of the cells. On the other hand, hyperosmotic concentrations of NaCl and mannitol increase freezing tolerance of protonemata.

At the same time, research by Takezawa and Minami (2004) identified genes coding for membrane transporter-like proteins. These newly identified proteins increase considerably following treatment with low temperatures, hyperosmotic solutes, or ABA. These genes are regulated by calmodulin.

Arachidonic Acid

Prins (1982) suggested that one reason small mammals eat mosses in winter is the content of **arachidonic acids**. These fatty acids make membranes more pliable and may make it easier for these rodents to run around on frozen ground and snow. But what do these do for bryophytes in winter? Does this extra flexibility also make it easier for them to survive? One protection against freezing is the ability to lose water, avoiding crystal formation that could damage membranes and organelles. With flexible membranes and withdrawal of water, the cells could shrink within the walls during the cold (and dry) period.

In ***Physcomitrella patens*** (Figure 87), production of arachidonic acid increases with higher concentrations of sugar (Chodok *et al*. 2010). Al-Hasan (1989) found that in ***Bryum bicolor*** (Figure 88) more arachidonic acid is produced at 5°C than at 25°C. Both of these studies support the production of arachidonic acid as winter approaches.

Figure 88. ***Bryum bicolor***, a species that produces more arachidonic acid at low temperatures than in warm ones. Photo by Michael Lüth, with permission.

Polyribosomes

Polyribosomes (cluster of ribosomes connected by a strand of messenger RNA and active in protein synthesis) respond to cooling temperatures. In the xerophytic moss ***Syntrichia ruralis*** (Figure 61-Figure 62), when temperatures descend to 2°C an accumulation of polyribosomes occurs while the single ribosomes decrease (Malek & Bewley 1978). This change in numbers reflects rearrangement, but does not involve a change in the number of ribosomal units. Slowly dried ***S. ruralis*** does not contain any polyribosomes when rehydrated, but these reform at 2, 8, and 20°C. Leucine rapidly incorporates into the protein when the plants are rehydrated at 20°C, but its incorporation is less dramatic at 2°C. Cold-hardened ***S. ruralis*** has no changes in the rate of protein synthesis at low temperatures (2°C). In fact, even in summer this species can carry out protein synthesis at low temperatures.

Summary

One of the dangers of frost damage is desiccation. Ice crystals on the inside of cells damage membranes and those on the outside pull water from the cells. Some bryophytes are protected by being encased in ice, preventing the formation of crystals and insulating against severe cold. Absence of vacuoles or having only small vacuoles can help to protect the interior of cells.

Many species survive winter and are ready for photosynthesis when the snow disappears, using the snowmelt water to rehydrate their tissues. Slow cooling, like slow drying may be important in survival. Extracellular freezing can protect against intracellular freezing. Some macromolecular substances can modify the shape of ice crystals in ways that do not damage the cells. Some ice-nucleating structures, made by the plants or available from the atmosphere, including proteins, create a small crystalline structure likewise protecting against damage from larger crystals. On the other hand, some ice crystals on the outsides of the cells can sequester water that is available at suitable temperatures. Desiccation can protect the cells by preventing crystal formation. Cell shrinkage helps to prevent crystal formation. Frequent freeze-thaw cycles, like dehydration-rehydration cycles, can damage the cells if the hydration and photosynthetic period is insufficient to repair membranes and accomplish a carbon gain.

Polyribosomes are active immediately following the freeze-thaw cycle. Lipids, starch bodies, sucrose, ABA, bibenzyls, bis(bibenzyls), and phenylpropanoids help to increase freezing and desiccation tolerance. Arachidonic acid helps to make membranes more pliable. These compounds permit some bryophytes to have seasonal tolerance. In desert habitats winter is often the best growing season because mosses remain hydrated for several days following rainfall events.

Some species become bleached from frost damage, but shoot tips and other parts may remain healthy and provide new growth in spring.

Acknowledgments

Thank you to Niels Klazenga, Marshall Crosby, and Pina Milne for helping me track down the current nomenclature for *Goniobryum enerve*. And of course a big thank you to all who have given me permission to use their images.

Literature Cited

Ahern, H., Walsh, K., Hill, T., and Moffett, B. F. 2007. Fluorescent pseudomonads isolated from Hebridean cloud and rain water produce biosurfactants but do not cause ice nucleation. Biogeosciences 4: 115-124.

Al-Hasan, R. H., El-Saadawi, W. E., Ali, A. M., and Radwan, S. S. 1989. Arachidonic and eicosapentaenoic acids in lipids of *Bryum bicolor* Dicks. Effects of controlled temperature and illumination. Bryologist 92: 178-182.

Alberdi, M., Bravo, L. A., Gutiérrez, A., Gidekel, M., and Corcuera, L. J. 2002. Ecophysiology of Antarctic vascular plants. Physiol. Plant. 115: 479-486.

Asada, T., Warner, B. G., and Banner, A. 2003. Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. Bryologist 106: 516-527.

Atanasiu, L. 1971. Photosynthesis and respiration of three mosses at winter low temperatures. Bryologist 74: 23-27.

Bailey, J. W. 1933. Mosses found near summer snowbanks. Bryologist 36: 8-11.

Barker, D. H., Stark, L. R., Zimpfer, J. F., McLetchie, N. D., and Smith, S. D. 2005. Evidence of drought-induced stress on biotic crust moss in the Mojave Desert. Plant Cell Environ. 28: 939-947.

Bates, J. 2006. Effects of simulated climatic changes on the bryophytes of a limestone grassland. Field Bryol. 89: 12-13.

Bauer, H., Kasper-Giebl, A., Loflund, M., Gieble, H., Hitzenberger, R., Zibuschka, F., and Puxbaum, H. 2002. The contribution of bacteria and fungal spores to the organic carbon content of cloud water, precipitation and aerosols. Atmos. Res. 64: 109-119.

Belland, R. J. 1983. A late snowbed bryophyte community in western Newfoundland, Canada. Can. J. Bot. 61: 218-223.

Bjerke, J. W., Bokhorst, S., Zielke, M., Callaghan, T. V., Bowles, F. W., and Phoenix, G. K. 2011. Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. J. Ecol. 99: 1481-1488.

Björk, R. G. 2007. Snowbed Biocomplexity: A Journey from Community to Landscape. Göteborg University, Göteborg.

Björk, R. G. and Molau, U. 2007. Ecology of alpine snowbeds and the impact of global change. Arct. Antarct. Alp. Res. 39: 34-43.

Buchner, O. and Neuner, G. 2010. Freezing cytorrhysis and critical temperature thresholds for photosystem II in the peat moss *Sphagnum capillifolium*. Protoplasma 243: 63-71.

Burch, J. 2003. Some mosses survive cryopreservation without prior pretreatment. Bryologist 106: 270-277.

Burch, J. and Wilkinson, T. 2002. Cryopreservation of protonemata of *Ditrichum cornubicum* (Paton) (sic) comparing the effectiveness of four cryoprotectant pretreatments. Cryo-letters 23(3): 197-208.

Chodok, P., Kanjana-Opas, A., and Kaewsuwan, S. 2010. The Plackett–Burman design for evaluating the production of polyunsaturated fatty acids by *Physcomitrella patens*. J. Amer. Oil Chem. Soc. 87: 521-529.

Christner, B., Morris, C., Foreman, C., Cai, R., and Sands, D. 2008. Ubiquity of biological ice nucleators in snowfall. Science 319: 1214-1215.

Davey, M. C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25-31.

Davey, M. C. and Rothery, P. 1996. Seasonal variation in respiratory and photosynthetic parameters in three mosses from the maritime Antarctic. Ann. Bot. 78: 719-728.

Deltoro, V. I., Calatayud, A., Morales, F., Abadía, A., and Barreno, E. 1999. Changes in net photosynthesis, chlorophyll fluorescence and xanthophyll cycle interconversions during freeze-thaw cycles in the Mediterranean moss *Leucodon sciuroides*. Oecologia 120: 499-505.

Despres, V. R., Nowoisky, J. F., Klose, M., Conrad, R., Andreae, M. O., and Poschl, U. 2007. Characterization of primary biogenic aerosol particles in urban, rural, and high-alpine air by DNA sequence and restriction fragment analysis of ribosomal RNA genes. Biogeosciences 4: 1127-1141.

Dilks, T. J. K. and Proctor, M. C. F. 1976. Seasonal variation in desiccation tolerance in some British bryophytes. J. Bryol. 2: 239-247.

Dorrepaal, E., Aerts, R., Cornelissen, J. H. C., Callaghan, T. V., and Logtestijn, R. S. P. van. 2004. Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. Global Change Biol. 10(1): 93-104.

Fletcher, M. 1982. Frost damage to bryophytes in cultivation. Bryol. Times 15: 3.

Flock, J. W. 1978. Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. Arct. Alp. Res. 10: 31-47.

Fornwall, M. D. and Glime, J. M. 1982. Cold and warm-adapted phases in *Fontinalis duriaei* Schimp. as evidenced by new assimilatory and respiratory responses to temperature. Aquat. Bot. 13: 165-177.

Forsum, Å, Laudon, H., and Nordin, A. 2008. Nitrogen uptake by *Hylocomium splendens* during snowmelt in a boreal forest. Ecoscience 15: 315-319.

Frahm, J.-P. 2006. Notulae Bryologicae Rhenanae 8: Moos über-wintert im Eis. Arch. Bryol. 13: 1.

Fukuta, N. 1966. Experimental studies of organic ice nuclei. J. Atmos. Sci. 23: 191-196.

Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes II. A comparative study of species of contrasted ecology. J. Ecol. 70: 525-536.

Gaberščik, A. and Martinčič, A. 1987. Seasonal dynamics of net photosynthesis and productivity of *Sphagnum papillosum*. Lindbergia 13: 105-110.

Gezelle, J. M. De. 2003. The Contribution of the *Porella*/*Nostoc* Association to the Nitrogen Budget of an Oregon Old-Growth Forest. Unpublished B. A. thesis, Reed College, Portland, Oregon, 32 pp.

Heber, U., Bilger, W., and Shuvalov, V. A. 2006. Thermal energy dissipation in reaction centres and in the antenna of photosystem II protects desiccated poikilohydric mosses against photo-oxidation. J. Exper. Bot. 57: 2993-3006.

Hébrard, J.-P., Foulquier, L., and Grauby, A. 1974. Appro che experimentale sur les possibilites de transfert du ^{90}Sr d'un substrat solide a une mousse terrestre: *Grimmia orbicularis* Bruch. Bull. Soc. Bot. France 121: 235-250.

Hedger, E. 2001. Environmental relationships of perichaetial and sporophyte production in *Andreaea* spp. in western Norway. J. Bryol. 23: 97-108.

Heegaard, E. 2002. A model of alpine species distribution in relation to snowmelt time and altitude. J. Veg. Sci. 13: 493-504.

Henderson-Begg, S. K., Hill, T., Thyrhaug, R., Khan, M., and Moffett, B. F. 2009. Terrestrial and airborne non-bacterial ice nuclei. Atmos. Sci. Lett. 10: 215-219.

Herbert, H. and Prins, T. 1982. Why are mosses eaten in cold environments only? Oikos 38: 374-380.

Herrnstadt, I. and Kidron, G. J. 2005. Reproductive strategies of *Bryum dunense* in three microhabitats in the Negev Desert. Bryologist 108: 101-109.

Horikawa, Y. and Ando, H. 1963. A review of the Antarctic species of *Ceratodon* described by Cardot. Hikobia 3: 275-280.

Hudson, M. A. and Brustkern, P. 1965. Resistance of young and mature leaves of *Mnium undulatum* (L.) to frost. Planta 66: 135-155.

Hynninen, V. 1986. Monitoring of airborne metal pollution with moss bags near an industrial source at Harjavalta, southwest Finland. Ann. Bot. Fenn. 23: 83-90.

Jägerbrand, A. K. 2011. Effects of climate change on tundra bryophytes. In: Tuba, Z., Slack, N. G., and Stark, L. R. Bryophyte Ecology and Climate Change. Cambridge University Press, Cambridge, pp. 211-236.

John, E. A. 1990. Fine scale patterning of species distributions in a saxicolous lichen community at Jonas Rockslide, Canadian Rocky Mountains. Holarct. Ecol. 13: 187-194.

Kaiser, G. B. 1921. Little journeys into mossland, II. – A February thaw. Bryologist 24: 5-6.

Kennedy, A. D. 1993. Photosynthetic response of the Antarctic moss *Polytrichum alpestre* Hoppe to low temperatures and freeze-thaw stress. Polar Biol. 13: 271-279.

Kieft, T. 1988. Ice nucleation activity in lichens. Appl. Environ. Microbiol. 54: 1678-1681.

Kieft, T. L. and Ahmadjian, V. 1989. Biological ice nucleation activity in lichen mycobionts and photobionts. Lichenologist 21: 355-362.

Kieft, T. L. and Ruscetti, T. 1990. Characterization of biological ice nuclei from a lichen. J. Bacteriol. 172: 3519-3523.

Laaka-Lindberg, S. and Heino, M. 2001. Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*. Oikos 94: 525-532.

Lai, Y. and Zhang, Y. 1994. The discovery and verification of new winter hosts of du-ensiform gall aphid, *Kaburagia rhusicola*. Forest Res. 7: 592-593.

Lenne, T., Bryant, G., Hocart, C. H., Huang, C. X., and Ball, M. C. 2010. Freeze avoidance: A dehydrating moss gathers no ice. Plant Cell Environ. 33: 1731-1741.

Li, X.-J. 1990. Study on the winter host mosses of gall aphids from China. In: Koponen, T. (ed.). Congress of East Asiatic Bryology, Helsinki. Programme and Abstracts, p. 26.

Lindow, S. 1983. The role of bacterial ice nucleation in frost injury to plants. Ann. Rev. Phytopathol. 21: 363-384.

Lindow, S. E., Hirano, S. S., Barchet, W. R., Arny, D. C., and Upper, C. D. 1982. Relationship between ice nucleation frequency of bacteria and frost injury. Plant Physiology 70: 1090-1093.

Long, D. G., Rothero, G. P., and Paton, J. A. 2003. *Athalamia hyalina* (Sommerf.) S. Hatt. in Scotland, new to the British Isles. J. Bryol. 25: 253-257.

Longton, R. E. 1981. Inter-populational variation in morphology and physiology in the cosmopolitan moss *Bryum argenteum* Hedw. J. Bryol. 11: 501-520.

Longton, R. E. 1988. Adaptations and strategies of polar bryophytes. Bot. J. Linn. Soc. 98: 253-268.

Longton, R. E. and Greene, S. W. 1969. The growth and reproductive cycle of *Pleurozium schreberi* (Brid.) Mitt. Ann. Bot. N. S. 33: 83-105.

Lösch, R., Kappen, L., and Wolf, A. 1983. Productivity and temperature biology of two snowbed bryophytes. Polar Biol. 1: 243-248.

Lovelock, C. E. and Robinson, S. A. 2002. Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. Plant Cell Environ. 25: 1239-1250.

Lovelock, C. E., Osmond, C. B., and Seppelt, R. D. 1995a. Photoinhibition in the Antarctic moss *Grimmia antarctici* Card when exposed to cycles of freezing and thawing. Plant Cell Environ. 18: 1295-1402.

Lovelock, C. E., Jackson, A. E., Melick, D. R., and Seppelt, R. D. 1995b. Reversible photoinhibition in Antarctic moss during freezing and thawing. Plant Physiol. 109: 955-961.

Malek, L. and Bewley, J. D. 1978. Effects of various rates of freezing on the metabolism of a drought-tolerant plant, the moss *Tortula ruralis*. Plant Physiol. 61: 334-338.

Markert, B. and Weckert, V. 1993. Time-and-site integrated long-term biomonitoring of chemical elements by means of mosses. Toxicol. Environ. Chem. 40: 43-56.

Marshall, W. A. 1996. Aerial dispersal of lichen soredia in the maritime Antarctic. New Phytol. 134: 523-530.

McDaniel, S. F. and Miller, N. G. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. Bryologist 103: 592-600.

McLetchie, D. N. 1999. Dormancy/nondormancy cycles in spores of the liverwort *Sphaerocarpos texanus*. Bryologist 102: 15-21.

Melick, D. R. and Seppelt, R. D. 1992. Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. Antarct. Sci. 4: 399-404.

Melick, D. R. and Seppelt, R. D. 1994. Seasonal investigations of soluble carbohydrates and pigment levels in Antarctic bryophytes and lichens. Bryologist 97: 13-19.

Melick, D. R., Hovenden, M. J., and Seppelt, R. D. 1994. Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, Continental Antarctica. Vegetatio 111: 71-87.

Miller, N. G. 1989. Late-Pleistocene *Anthelia* (Hepaticae), an arctic-alpine, snow-bed indicator at a low elevation site in Massachusetts, U. S. A. J. Bryol. 15: 583-588.

Miller, N. G. and Howe Ambrose, L. J. 1976. Growth in culture of wind-blown bryophyte gametophyte fragments from arctic Canada. Bryologist 79: 55-63.

Milne, J. 2001. Reproductive biology of three Australian species of *Dicranoloma* (Bryopsida, Dicranaceae): Sexual reproduction and phenology. Bryologist 104: 440-452.

Minami, A., Nagao, M., Arakawa, K., Fujikawa, S., and Takezawa, D. 2003. Abscisic acid-induced freezing tolerance in the moss *Physcomitrella patens* is accompanied by increased expression of stress-related genes. J. Plant Physiol. 160: 475-483.

Minami, A., Nagao, M., Ikegami, K., Koshiba, T., Arakawa, K., Fujikawa, S., and Takezawa, D. 2005. Cold acclimation in bryophytes: Low-temperature-induced freezing tolerance in *Physcomitrella patens* is associated with increases in expression levels of stress-related genes but not with increase in level of endogenous abscisic acid. Planta 220: 414-423.

Moffett, B. F., Hill, T., and Henderson-Begg, S. K. 2009. Major new sources of biological ice nuclei. The Smithsonian/NASA Astrophysics Data System.

Möhler, O., Benz, S., Saathoff, H., Schnaiter, M., Wagner, R., Schneider, J., Walter, S., Ebert, V., and Wagner, S. 2008. The effect of organic coating on the heterogeneous ice nucleation efficiency of mineral dust aerosols. Environ. Res. Lett. 3(2): 8 pp.

Nagao, M., Minami, A., Arakawa, K., Fujikawa, S., and Takezawa, D. 2001. Abscisic acid and low temperature increased gene expression along with enhancement of freezing tolerance n *Physcomitrella patens*. In: Shin, J. S. and Sasebe, M. (eds.). Moss 2001: An International

Meeting on Moss Biology. National Institute for Basic Biology, Okazaki, Japan, p. 70.

Nagao, M., Oku, K., Sakurai, M., Kim, Y.-M., Kimura, A., Minami, A., Arakawa, K., Fujikawa, S., and Takezawa, D. 2003. Increase in soluble sugars in protonema cells of *Physcomitrella patens* by ABA treatment in association with enhancement of freezing tolerance. J. Plant Res. 116 (Suppl.): 79-80.

Nagao, M., Minami, A., Arakawa, K., Fujikawa, S., Takezawa, D. 2005. Rapid degradation of starch in chloroplasts and concomitant accumulation of soluble sugars associated with ABA-induced freezing tolerance in the moss *Physcomitrella patens*. J. Plant Physiol. 162: 169-180.

Nagoa, M., Oku, Kl., Minami, A., Mizuno, K., Sakurai, M., Arakawa, K., Funikawa, S., Takezawa, D. 2006. Accumulation of theanderose in association with development of freezing tolerance in the moss *Physcomitrella patens*. Phytochemistry 67: 702-709.

NZOR. 2015. *Mnium*. Accessed 8 April 2015 at <http://www.nzor.org.nz/names/9fd5a2ff-93a9-4a7e-9441-e91db601c283>.

Oldenhof, H., Wolkers, W. F., Bowman, J. L., Talin, F., and Crow, J. H. 2006. Freezing and desiccation tolerance in the moss *Physcomitrella patens*: An *in situ* Fourier transform infrared spectroscopic study. Biochim. Biophys. Acta 1760: 1226-1234.

Oloffson, J., Moen, J., and Oksanen, L. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. Oikos 96: 265-272.

Pannewitz, S., Schlensog, M., Green, T. G. A., Sancho, L. G., and Schroeter, B. 2003. Are lichens active under snow in continental Antarctica? Oecologia 135: 30-38.

Pouleur, S., Richard, C., Martin, J., and Antoun, H. 1992. Ice nucleation activity in *Fusarium acuminatum* and *Fusarium avenaceumt*. Appl. Environ. Microbiol. 58: 2960-2964.

Priddle, J. 1979. Morphology and adaptation of aquatic mosses in an Antarctic lake. J. Bryol. 10: 517-529.

Prins, H. H. T. 1982. Why are mosses eaten in cold environments only? Oikos 38: 374-380.

Proctor, M. C. 2000. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Proctor, M. C. F. 2004. How long must a desiccation-tolerant moss tolerate desiccation? Some results of two years' data logging on *Grimmia pulvinata*. Physiol. Plant. 122: 21-27.

Raymond, J. A. and Fritsen, C. H. 2001. Semipurification and ice recrystallization inhibition activity of ice-active substances associated with Antarctic photosynthetic organisms. Cryobiology 43: 63-70.

Rochefort, L., Campeau, S., and Bugnon, J.-L. 2002. Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*? Aquat. Bot. 74: 327-341.

Rothero, G. 2007. Saying goodbye to our Arctic? The future of snowbed vegetation in Scotland. Field Bryol. 91: 40-41.

Rowntree, J. K., Duckett, J. G., Mortimer, C. L., Ramsay, M. M., and Pressel, S. 2007. Formation of specialized propagules resistant to desiccation and cryopreservation in the threatened moss *Ditrichum plumbicola* (Ditrichales, Bryopsida). Ann. Bot. 100: 483-496.

Rütten, D. and Santarius, K. A. 1992. Relationship between frost tolerance and sugar concentration of various bryophytes in summer and winter. Oecologia 91: 260-265.

Rütten, D. and Santarius, K. A. 1993. Cryoprotection of *Plagiomnium affine* induced by various natural and artificial substances. Can. J. Bot. 71: 793-798.

Saruwatari, M., Takio, S., and Ono, K. 1999. Low temperature-induced accumulation of eicosapentaenoic acids in *Marchantia polymorpha* cells. Phytochemistry 52: 367-372.

Schlensog, M., Pannewitz, S., Green, T. G. A., and Schroeter, B. 2004. Metabolic recovery of continental Antarctic cryptogams after winter. Polar Biol. 27: 399-408.

Schuster, R. and Greven, H. 2007. A long-term study of population dynamics of tardigrades in the moss *Rhytidiadelphus squarrosus* (Hedw.) Warnst. J. Limnol. 66(Suppl. 1): 141-151.

Segreto, R., Hassel, K., Bardal, R., and Stenoien, H. K. 2010. Desiccation tolerance and natural cold acclimation allow cryopreservation of bryophytes without pretreatment or use of cryoprotectants. Bryologist 113: 760-769.

Seppelt, R. D. 1997. Vacuoles. Bryonet discussion on 14 November 1997.

Seppelt, R. D. and Laursen, G. A. 1999. *Riccia cavernosa* Hoffm. emend Raddi, new to the Arctic and the bryoflora of Alaska. Hikobia 13: 71-76.

Seppelt, R. and Ochyra, R. 2008. Moss amongst the ice – the forests of Antarctica. Field Bryol. 94: 39-43.

Seppelt, R. D. and Selkirk, P. M. 1984. Effects of submersion on morphology and the implications of induced environmental modification on the taxonomic interpretation of selected Antarctic moss species. J. Hattori Bot. Lab. 55: 273-279.

Seppelt, R. D., Green, T. G. A., Schwarz, A. M., and Frost, A. 1992. Extreme southern locations for moss sporophytes in Antarctica. Antarct. Sci. 4: 37-39.

Shirasaki, H. 1984. Ecological distribution of *Bryoxiphium norvegicum* subsp. *japonicum*. J. Phytogeogr. Tax. 32: 59-67.

Shirasaki, H. 1987. Ecological distributions of *Bazzania trilobata* S. Gray and *B. yoshinagana* Hatt. (Hepaticae). Soc. Stud. Phytogeogr. Tax. 35(1): 27-35.

Shirasaki, H. 1996. Distribution and ecology of *Ricciocarpos natans* in Niigata Prefecture and its adjacent regions, central Japan. Proc. Bryol. Soc. Japan 6(11): 209-215.

Shirasaki, H. 1997. Distribution and ecology of *Dichelyma japonicum* in the deep snow-covered district of Niigata Prefecture and its adjacent regions, central Japan. Bryol. Res. 7(2): 44-49.

Shirasaki, H. 1998. Distribution and ecology of *Trachycystis flagellaris* and *T. microphylla* in Niigata Prefecture and its adjacent regions, central Japan. Bryol. Res. 7(5): 139-145.

Slack, N. G., Duckett, J. G., and Capers, R. S. 2013. Monitoring alpine bryophytes and snowbed communities in Northeastern United States. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.

Sonesson, M., Carlsson, B. Å., Callaghan, T. V., Halling, S., Björn, L. O., Bertgren, M., and Johanson, U. 2002. Growth of two peat-forming mosses in subarctic mires: Species interactions and effects of simulated climate change. Oikos 99: 151-160.

Stark, L. R. 2002. Skipped reproductive cycles and extensive sporophyte abortion in the desert moss *Tortula inermis* correspond to unusual rainfall patterns. Can. J. Bot. 80: 533-542.

Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.

Stark, L. R. and Brinda, J. C. 2015. Developing sporophytes transition from an inducible to a constitutive ecological strategy of desiccation tolerance in the moss *Aloina*

ambigua: Effects of desiccation on fitness. Ann. Bot. 115: 593-603.

Startsev, N. A., Lieffers, V. J., and McNabb, D. H. 2007. Effects of feathermoss removal, thinning and fertilization on lodgepole pine growth, soil microclimate and stand nitrogen dynamics. Forest Ecol. Mgmt. 240: 79-86.

Takezawa, D. and Minami, A. 2004. Calmodulin-binding proteins in bryophytes: Identification of abscisic acid-, cold-, and osmotic stress-induced genes encoding novel membrane-bound transporter-like proteins. Biochem. Biophys. Res. Commun. 317: 428-436.

Takezawa, D., Komatsu, K., and Sakata, Y. 2011. ABA in bryophytes: How a universal growth regulator in life became a plant hormone? J. Plant Res. 124: 437-453.

Tearle, P. V. 1987. Cryptogamic carbohydrate release and microbial response during spring freeze-thaw cycles in Antarctic fellfield sites. Soil Biol. Biochem. 19: 381-390.

Thomas, W. 1981. Entwicklung eines immissionsme b systems fur PCA, chlorkohlenwasserstoffe und spurenmetalle mittels epiphytischer Moose – angewandt auf den Raum Bayern. Bayreuther Geowiss. Arb., 142 pp.

Tormo, R., Recio, D., Silva, I., and Munoz, A. F. 2001. A quantitative investigation of airborne algae and lichen soredia obtained from pollen traps in South West Spain. Eur. J. Phycol. 36: 385-390.

Trynoski, S. E. and Glime, J. M. 1982. Direction and height of bryophytes on four species of northern trees. Bryologist 85: 281-300.

Ueno, T., Imura, S., and Kanda, H. 2001. Colony form and shoot morphology of *Sanionia uncinata* (Hedw.) Loeske growing in different water conditions in the high Arctic, Spitsbergen, Svalbard. Bryol. Res. 8: 1-6.

Woolgrove, C. E. and Woodin, S. J. 1994. Relationships between the duration of snowlie and the distribution of bryophyte communities within snowbeds in Scotland. J. Bryol. 19: 253-260.

Woolgrove, C. E. and Woodin, S. J. 1996. Ecophysiology of a snow-bed bryophyte *Kiaeria starkei* during snowmelt and uptake of nitrate from meltwater. Can. J. Bot. 74: 1095-1103.

Xie, C.-F. and Lou, H.-X. 2009. Secondary metabolites in bryophytes: An ecological aspect. Chem. Biodiv. 6: 303-312.

Zachariassen, K. E. and Kristiansen, E. 2000. Ice nucleation and antinucleation in nature. Cryobiology 41: 257-279.

CHAPTER 7-10
WATER RELATIONS: SNOW ECOLOGY

TABLE OF CONTENTS

Snow Effects 7-10-2
Snowbed Communities 7-10-4
Growth Form Variability 7-10-10
Duration of Snowbeds 7-10-13
Snowmelt 7-10-13
Mechanical Effects 7-10-18
Freeze-thaw Cycles 7-10-18
Winter Short-term Warming Events 7-10-20
Protection from Light Damage 7-10-20
Winter Growth 7-10-21
Winter and Reproduction 7-10-26
Asexual Survival 7-10-28
Sympatric Differences 7-10-28
Effects of Bryophytes on their Communities in Winter 7-10-29
Winter Dispersal 7-10-30
Pollution Effects – Vital Water or Deadly Poisons? 7-10-30
Summary 7-10-31
Acknowledgments 7-10-31
Literature Cited 7-10-31

CHAPTER 7-10
WATER RELATIONS: SNOW ECOLOGY

Figure 1. Late snowbeds in an alpine habitat in the Khibiny Mountains, Russia. ***Bucklandiella microcarpum*** is in the foreground. Photo by Michael Lüth, with permission.

Snow Effects

Snow can contribute in multiple ways to enhance the productivity. We know little about productivity of bryophytes under snow. What we do know is that light can penetrate snow, but that the light quality is altered. We know that snowmelt provides moisture, and that this melt can occur while the snow pack is still present, even in the middle of winter. We know that the snow can buffer the temperature, maintaining it close to 0°C. Dorrepall *et al*. (2004) demonstrated that ***Sphagnum fuscum*** (Figure 2) experienced an enhancement of 33% in productivity as a result of winter snow addition, while, nevertheless, not increasing growth in length.

Even in areas with considerable snow, bare areas exist, often as a result of winds that clear the snow. Some of these surfaces are rock surfaces that protrude, making them vulnerable to those wind movements of the snow (John 1990). One moss species capable of living in such exposed areas is ***Grimmia longirostris*** (Figure 3) in the Canadian Rocky Mountains.

Figure 2. ***Sphagnum fuscum***, a moss that experiences greater productivity as a result of winter snow. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.

Figure 3. ***Grimmia longirostris***, a species of exposed areas. Photo by Michael Lüth, with permission.

I have long suspected that at least some bryophytes are able to carry out photosynthesis under snow as long as it is not too deep for sufficient light penetration. Pannewitz *et al*. (2003) demonstrate that photosynthesis under the snow occurs in lichens. The snow cover provides effective insulation against the bitter cold of the Antarctic atmosphere, protecting both the mosses and the lichens. But in spring, this insulation proves to be detrimental. It retains the severe cold of winter and prevents the bryophytes from benefitting from the early warming of the air. This delay can last 10-14 days. Furthermore, the hydration provided to the lichens by the snow lasts only briefly once the snow disappears, providing only a brief period for photosynthetic activity. Is this same shortening of the photosynthetic period in effect for bryophytes, or are they able to retain the water longer?

In our study of the bryophytes on trees in the Keweenaw Peninsula of Michigan, USA, we found that those about 1 m above the ground were most common on the south sides of the trees (Trynoski & Glime 1982). We attributed this to a combination of winds from the north and sufficient light and moisture for these bryophytes to have photosynthesis in winter. Trees always have a narrow funnel of space between them and the snow (Figure 4). In this area where snow on the ground reaches a meter or move depth, the snow is an insulator. Dark-colored bark is able to absorb heat and the funnel remains somewhat humid. Light is able to penetrate. I have no measurements of growth or photosynthetic activity for these epiphytes – that needs to be done.

Figure 4. Snow-covered forest showing space between snow and tree trunk. Photo by Janice Glime.

Snow can affect the distribution of species. For example, in Japan ***Bazzania trilobata*** (Figure 5-Figure 7) grows on ground that is well drained all year and is typically sunny (Shirasaki 1987). ***Bazzania yoshinagana*** (Figure 8), on the other hand, grows on the forest floor in densely shaded coniferous forests. It spends its winter covered with deep snow that insulates it from freezing and provides it with moisture.

Figure 5. ***Bazzania trilobata*** habitat where it lives in well-drained locations. Photo by Dick Haaksma, with permission.

Figure 6. ***Bazzania trilobata***, a species of well-drained locations. Photo by Michael Lüth, with permission.

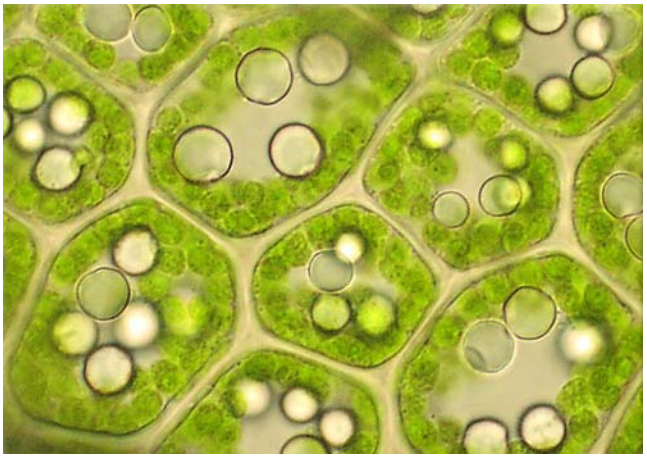

Figure 7. ***Bazzania trilobata*** leaf cells showing spherical oil bodies that may help in surviving desiccation. Photo by Walter Obermayer, with permission.

Figure 8. ***Bazzania yoshinagana***, a species of dense forest shade where it spends its winter under steep snow. Photo by Li Zhang, with permission.

Snowbed Communities

"Areas which experience prolonged snowlie and possess a distinctive bryophyte-dominated vegetation are termed snowbeds" (Woolgrave & Woodin 1996). Snowbeds (Figure 9) create their own unique characters. They shorten the growing season but can extend the period of hydration. Some bryophytes are dependent on these sources of hydration. On the Antarctic peninsulas the snow cover and site exposure seem to define the plant distribution (Melick *et al*. 1994).

Figure 9. Late snowbed at Bjoerndalen, Spitzbergen. Photo by Michael Lüth, with permission.

Snowbeds form in crevices and depressions in alpine regions (Figure 9). These are among the last areas to lose their snow, often near the end of the growing season. Nevertheless, some species grow only in these areas (Björk & Molau 2007). One such species that indicates a location with late snowbeds is the liverwort ***Anthelia*** (Figure 10), a genus whose fossils also indicate areas of late-lying snow in the late-Pleistocene landscape (Miller 1989). These snowbeds provide both a steady water supply and a steady nutrient supply to the adjacent plant communities. Because of this dependence, these communities are particularly vulnerable to climate warming.

Figure 10. ***Anthelia juratzkana***, an indicator of late snowbeds. Photo by Hermann Schachner, through Creative Commons.

Many of the alpine bryophytes display adaptations that make their snowbed habitats tenable. ***Andreaea nivalis*** (Figure 11-Figure 12) is a reddish moss that hangs where snow water glides over the rocks and cliffs (Bailey 1933). Even its name (*nivalis*) means snow-covered. ***Brachymenium erectum*** (Figure 13) grows in snow water in alpine areas and disintegrates so rapidly after maturity that it is easy to miss it altogether. ***Pohlia ludwigii*** (Figure 14-Figure 15) lives in or near snow water. ***Pohlia filum*** (Figure 16) grows in snow water on the south side of Mount Rainier, Washington, USA, and produces brood bodies (Figure 17) in the snow water. ***Polytrichastrum sexangulare*** (Figure 18-Figure 20) likewise lives near the snow. Its setae begin to elongate before the snow is completely gone and as a result they become trailing and twisted (Figure 20). ***Bryum muehlenbeckii*** (Figure 21) has deep red leaves and stems, probably protecting it from UV radiation, and possibly increasing its temperature in its cold habitat near the snowbeds. ***Pohlia wahlenbergii*** var. ***glacialis*** (Figure 22-Figure 23), by contrast, has whitish leaves. On Mt. Rainier it covers large expanses that are wet with snow water. ***Meiotrichum lyallii*** (Figure 24) becomes visible at high elevations as soon as the snow disappears and is common on the higher slopes of Mt. Rainier. All of these bryophytes are acrocarpous mosses. Only ***Isopterygiopsis pulchella*** (Figure 25) is a pleurocarpous snow lover associated with these snowbeds. In all cases, it is likely that these bryophytes are non-competitors with tracheophytes and that take advantage of their C_3 photosynthesis to grow in the cold temperatures when adequate moisture is available.

Figure 11. ***Andreaea nivalis*** in its alpine habitat. Photo by Michael Lüth, with permission.

Figure 12. ***Andreaea nivalis*** in a location where it receives water that glides over rocks and cliffs. Photo by Michael Lüth, with permission.

Figure 13. ***Brachymenium*** in India. ***Brachymenium erectum*** is short-lived in alpine snowbed runoff. Photo by Michael Lüth, with permission.

Figure 14. ***Pohlia ludwigii*** in its late snowmelt water habitat. Photo by Michael Lüth, with permission.

Figure 15. ***Pohlia ludwigii***, a moss that thrives in snowmelt water. Photo by Michael Lüth, with permission.

Figure 16. ***Pohlia filum*** growing in wet soil from snowmelt. Photo by Michael Lüth, with permission.

Figure 17. ***Pohlia filum*** showing the bulbils that are produced while it grows in snowmelt water. Photo by Michael Lüth, with permission.

Figure 18. ***Polytrichum sexangulare*** at alpine lake in Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Polytrichastrum sexangulare***, a late snowbed bryophyte. Photo by Martin Hutten, with permission.

Figure 20. ***Polytrichastrum sexangulare*** showing crooked and twisted setae from developing under snow. Photo by Michael Lüth, with permission.

Figure 21. ***Bryum muehlenbeckii*** in snowmelt water on rock. Note the red color, a common character of alpine bryophytes. Photo by Michael Lüth, with permission.

Figure 22. ***Pohlia wahlenbergii*** var ***glacialis*** in its snowmelt habitat. Photo by Michael Lüth, with permission.

Figure 23. ***Pohlia wahlenbergii*** var ***glacialis***, a species that thrives in snow water. Photo by Michael Lüth, with permission.

Figure 24. ***Meiotrichum lyallii*** with capsules, looking somewhat flattened after snowmelt. Photo by Paul Wilson, with permission.

Figure 25, ***Isopterygiopsis pulchella***, the only pleurocarpous moss living in late snowbeds on Mt. Rainier, USA. Photo by Jan-Peter Frahm, with permission.

In Scotland, some of these same species are dependent on the snowbeds (Rothero 2007). These include ***Andreaea nivalis*** (Figure 11-Figure 12), ***Polytrichum sexangulare*** (Figure 18-Figure 20), ***Kiaeria falcata*** (Figure 26-Figure 27), ***Anthelia juratzkana*** (Figure 10), and ***Pohlia ludwigii*** (Figure 14-Figure 15). Additionally, snowbeds in the UK are habitats for ***Racomitrium heterostichum*** (Figure 28), ***Marsupella brevissima*** (Figure 29-Figure 30), ***Kiaeria starkei*** (Figure 31), ***Moerckia blyttii*** (Figure 32), ***Pleurocladula albescens*** (Figure 33-Figure 34), ***Marsupella arctica***, and ***Marsupella condensata*** (Figure 35). The flushes and mires resulting from melting snowbeds also support growths of ***Pohlia wahlenbergii*** var. ***glacialis*** (Figure 22-Figure 23), ***Scapania paludosa*** (Figure 36), and occasionally ***Sphagnum riparium*** (Figure 37) and ***S. lindbergii*** (Figure 38-Figure 39).

Figure 26. ***Kiaeria falcata*** habitat where snowbeds are important to this species. Photo by Michael Lüth, with permission.

Figure 27. ***Kiaeria falcata***, a moss dependent on snowbeds. Photo by Michael Lüth, with permission.

Figure 28. ***Racomitrium heterostichum***, a snowbed species. Photo by J. C. Schou, through Creative Commons.

Figure 29. ***Marsupella brevissima*** habitat. Photo by Michael Lüth, with permission.

Figure 30. ***Marsupella brevissima***, a snowbed liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 31. ***Kiaeria starkei*** with capsules, a late snowbed moss. Photo by Rosemary Taylor, with permission.

Figure 32. ***Moerckia blyttii***, a snowbed bryophyte. Photo by Michael Lüth, with permission.

Figure 33. ***Pleuroclada albescens*** in a snowmelt bed in Norway. Photo by Michael Lüth, with permission.

Figure 34. ***Pleuroclada albescens***, a snowbed liverwort. Photo by Michael Lüth, with permission.

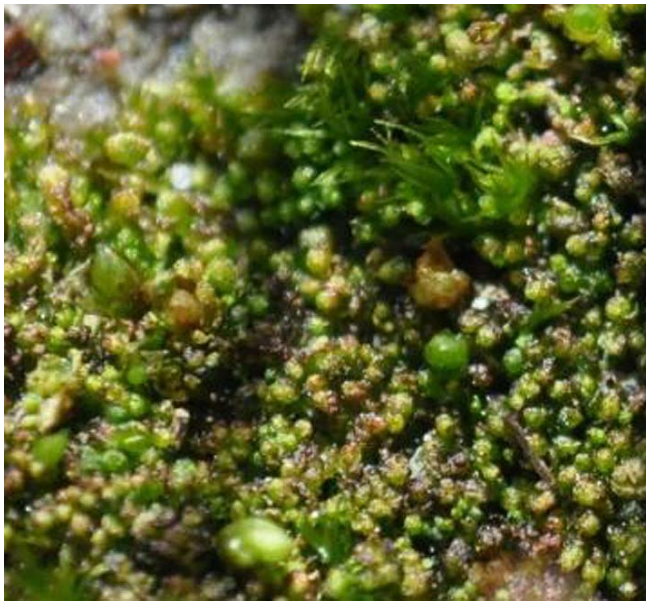

Figure 35. ***Marsupella condensata***, a species that lives in snowbeds in the UK. Photo by Andrew Hodgson, with permission.

Figure 36. ***Scapania paludosa***, a species that benefits fro snowmelt flushes. Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum riparium***, a species sometimes found in late snowbeds. Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Sphagnum lindbergii*** where it gains water from spring flushes. Photo by Michael Lüth, with permission.

Figure 39. ***Sphagnum lindbergii***, a species that sometimes benefits from snowbed water. Photo by Michael Lüth, with permission.

In snowbeds, more than 40% of the cover is often comprised of bryophytes (Jägerbrand 2011). This may be as little as 3% of the exposed area during early melt to 80% in the late-melting areas. Björk (2007) found 26 species that grow mostly in snowbeds, 13 of which are found only in those areas. In a late snowbed in western Newfoundland, Canada, Belland (1983) found some of the same species associations as named above for the UK. In particular, ***Andreaea nivalis*** (Figure 11-Figure 12) was common in late snowbeds. Belland found 49 bryophyte species in the eight late snowbeds he investigated. Other dominant species included ***Kiaeria falcata*** (Figure 26-Figure 27), ***Moerckia blyttii*** (Figure 32), and a species of ***Trematodon*** (Figure 40). The uniqueness of this habitat is demonstrated by the disjunct distribution for 13 of these species between western and eastern North America. Eleven of the species are characteristic of snowbed habitats throughout most of the world.

Figure 40. ***Trematodon longicollis***, in a genus represented in snowbeds in Newfoundland, Canada. Photo by Michael Lüth, with permission.

The unique combination of temperature regime and moisture support some of the rare species of the world. On Mt. Washington, New Hampshire, USA, Slack *et al*. (2013) found ***Haplomitrium hookeri*** (Figure 41), ***Aulacomnium turgidum*** (Figure 42-Figure 44), ***Dicranum elongatum*** (Figure 43), and ***Pseudocalliergon trifarium*** (Figure 45) – all rare species in the northeastern USA.

Figure 41. ***Haplomitrium hookeri*** in a late snowbed in Wales. Photo by Janice Glime.

Figure 42. ***Aulacomnium turgidum*** in an alpine area of Norway. Photo by Michael Lüth, with permission.

Figure 43. ***Dicranum elongatum***, a rare species on Mt. Washington, NH, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 44. ***Aulacomnium turgidum***, a rare species that survives on Mt. Washington, New Hampshire, USA. Photo by Michael Lüth, with permission.

Figure 45. ***Pseudocalliergon trifarium***, a rare species that survives the harsh climate on Mt. Washington, NH, USA. Photo by Andrew Hodgson, with permission.

Growth Form Variability

Snowbeds can create unusual growth forms. For example, in the high Arctic of Spitsbergen, the fellfield type of ***Sanionia uncinata*** (Figure 46-Figure 48) had few branchless shoots and formed dense colonies, leading to better desiccation avoidance (Ueno *et al.* 2001). The snowbed type had many branchless shoots and more sparse colonies. Furthermore, there were fewer branches in the upper part of the shoot than in the lower part in the snowbeds. Was this a response to the snow, possibly damaging branch buds, or was the more dense branching in the fellfield an adaptation selected to permit survival in the drier climate there?

Figure 46. ***Sanionia uncinata*** alpine habitat in Europe. Photo by Michael Lüth, with permission.

Figure 47. ***Sanionia uncinata*** with capsules in runoff area. Photo by Michael Lüth, with permission.

Figure 48. ***Sanionia uncinata*** with capsules and showing pinnate growth form. Photo by Michael Lüth, with permission.

The multiple growth forms of some species in the Antarctic seem to be a response to submersion (Seppelt & Selkirk 1984). For example, ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) was originally named as ***Bryum algens*** there due to its different growth form. ***Calliergon sarmentosum*** (Figure 51-Figure 52) assumes a different morphology when shoots develop under water or in damp conditions (Priddle 1979). ***Bryum argenteum*** (Figure 53-Figure 54) in the Antarctic assumes longer and narrower leaves with increased cell size in etiolated shoots (Longton 1981; Seppelt & Selkirk 1984), perhaps due to submersion, or possibly due to growth in the reduced light under snow. ***Ceratodon purpureus*** (Figure 55-Figure 60) lives in shallow lakes in the Antarctic and was originally known as ***Ceratodon minutifolius*** there, differing in leaf shape and leaf apex (Horikawa & Ando 1963; Seppelt & Selkirk 1984).

Figure 49. ***Bryum pseudotriquetrum*** in the Antarctic, a moss with many growth forms. Photo courtesy of Catherine Beard.

Figure 50. ***Bryum pseudotriquetrum*** beside a stream, showing a typical growth form in the North Temperate Zone. Photo by Michael Lüth, with permission.

Figure 51. ***Calliergon sarmentosum*** mountain habitat in Europe. Photo by Michael Lüth, with permission.

Figure 52. ***Calliergon sarmentosum*** aquatic growth form. Photo by Michael Lüth, with permission.

Figure 53. ***Bryum argenteum*** from the Neotropics, exhibiting the broader leaves typical there. Photo by Michael Lüth, with permission.

Figure 54. ***Bryum argenteum*** from alpine area in Europe where it exhibits longer, narrower leaves than plants from the tropics. Photo by Michael Lüth, with permission.

Figure 55. ***Ceratodon purpureus*** in Antarctica. Photo by Rod Seppelt, with permission.

Figure 56. ***Ceratodon purpureus*** in Antarctica. (Blackish mosses at right are ***Bryum pseudotriquetrum***.) Photo by Rod Seppelt, with permission.

Figure 57. Submerged ***Ceratodon purpureus*** in the Antarctic. Bubbles from photosynthesis here create a condition known as **pearling**. Photo courtesy of Rod Seppelt.

Figure 58. Open growth of well-hydrated ***Ceratodon purpureus***. Photo by Michael Lüth, with permission.

Figure 59. Cushions of ***Ceratodon purpureus*** in the mountains of Norway. Photo by Michael Lüth, with permission.

Figure 60. ***Ceratodon purpureus*** dry among rocks in Michigan, USA. Photo by Janice Glime.

Duration of Snowbeds

The duration of the snowbeds separates communities in Scotland (Woolgrove & Woodin 1994). Prolonged snowlie has negative effects on the ***Marsupella-Anthelia*** community (Figure 29-Figure 30, Figure 35; Figure 10). On the other hand, the ***Polytrichum-Kiaeria*** (Figure 18-Figure 20; Figure 26-Figure 27) community is positively affected by its prolongation. ***Pohlia*** (Figure 14-Figure 16, Figure 22-Figure 23) seems less affected by the duration, but the substrate moisture content is important for it.

Snowmelt

Kaiser (1921) describes his "journey into mossland" during a February thaw in Pennsylvania, USA. So many mosses appeared, bright green, and ready to grow. These winter survivors, especially along streambanks, included ***Plagiomnium cuspidatum*** (Figure 61-Figure 62), ***Leucobryum glaucum*** (Figure 63-Figure 67), ***Bryoandersonia illecebra*** (Figure 68-Figure 69), ***Dicranum scoparium*** (Figure 70-Figure 71), ***Plagiomnium ciliare*** (Figure 72), ***Rhizomnium punctatum*** (Figure 73), ***Conocephalum conicum*** (Figure 74), ***Marchantia polymorpha*** (Figure 75), ***Pellia epiphylla*** (Figure 76), ***Atrichum*** (Figure 77), ***Dicranella*** (Figure 78), ***Pohlia nutans*** (Figure 79-Figure 80), and ***Bartramia pomiformis*** (Figure 81-Figure 82), among others, all benefitting from the snowmelt moisture.

Figure 61. ***Plagiomnium cuspidatum*** hydrated, a moss that survives snow cover to regain photosynthesis in spring. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Plagiomnium cuspidatum*** dry. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 63. ***Leucobryum glaucum*** on edge of crevice where it escapes the leaf litter. This site benefits from runoff, but can also suffer exposure. Photo by Janice Glime.

Figure 64. ***Leucobryum glaucum***, one of the mosses that is ready to photosynthesize when the snow melts. Photo courtesy of Eileen Dumire.

Figure 65. ***Leucobryum glaucum*** showing the whitish color due to hyaline cells that help to keep the photosynthetic cells hydrated. Photo by Janice Glime.

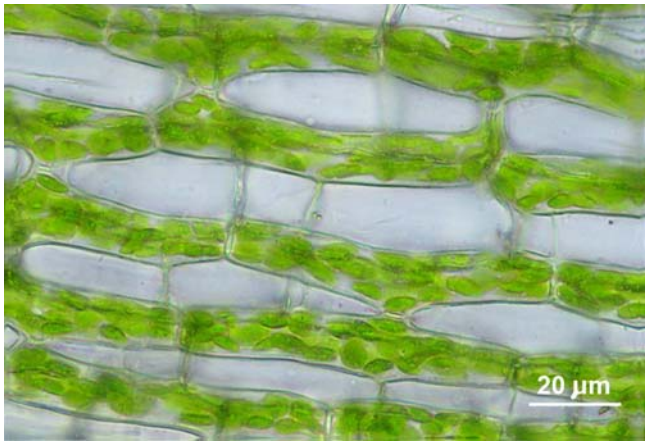

Figure 66. ***Leucobryum glaucum*** showing photosynthetic and hyaline leaf cells. Photo by David Wagner, with permission.

Figure 67. ***Leucobryum glaucum*** leaf cross section showing photosynthetic and hyaline cells. Photo by Walter Obermayer, with permission.

Figure 68. ***Bryoandersonia illecebra***, a moss that one can find when the snow melts in Ohio, USA. Photo by Bob Klips, with permission.

Figure 69. ***Bryoandersonia illecebra*** on tree, a species of vertical surfaces. Photo by Bob Klips, with permission.

Figure 70. ***Dicranum scoparium*** in early autumn, a moss that overwinters and looks bright when the snow melts. Photo by Janice Glime.

Figure 71. ***Dicranum scoparium*** with capsules. Photo by Michael Lüth, with permission.

Figure 72. ***Plagiomnium ciliare*** with antheridia, a moss that overwinters and is ready to grow when the snow leaves. Photo by Robert Klips, with permission.

Figure 73. ***Rhizomnium punctatum*** looking etiolated after its winter snow cover. Photo by Michael Lüth, with permission.

Figure 74. ***Conocephalum conicum***, a liverwort that is active in early spring. Photo by Janice Glime.

Figure 75. ***Marchantia polymorpha*** with gemmae cups, a liverwort that is active when the snow melts. Photo by David T. Holyoak, with permission.

Figure 76. ***Pellia epiphylla*** in the mountains of Wales. Photo by Janice Glime.

Figure 77. ***Atrichum undulatum*** in snow, a species that has a distinct increase in cold tolerance from summer to winter and is ready for photosynthesis when the snow melts. Photo by Michael Lüth, with permission.

Figure 78. ***Dicranella heteromalla***, a soil bank moss that is ready to grow when the snow melts. Photo by Michael Lüth, with permission.

Figure 79. ***Pohlia nutans*** at snowmelt time in the Khibiny Mountains, Russia. Photo by Michael Lüth, with permission.

Figure 80. ***Pohlia nutans***, one of the first plants to be seen in spring. Photo by Michael Lüth, with permission.

Figure 81. ***Bartramia pomiformis*** in its typical cliff-hanger habitat. Photo by Janice Glime.

Figure 82. ***Bartramia pomiformis***, a moss that is green in early spring. Photo by Michael Lüth, with permission.

Gaberščik and Martinčič (1987) demonstrated seasonal changes in growth of ***Sphagnum papillosum*** (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing season, a time when water is usually plentiful. During winter months, the photosynthetic activity declines and ceases completely in February.

Figure 83. ***Sphagnum papillosum*** on exposed rock where it can benefit from spring snowmelt runoff. Photo by Michael Lüth, with permission.

Figure 84. ***Sphagnum papillosum*** in a flush created by melting snow. This one is still wet in late July in the mountains of Wales. Photo by Janice Glime.

Figure 85. ***Sphagnum papillosum***, shown here with sundews. This ***Sphagnum*** species has seasonal changes in growth, with photosynthetic activity declining in winter in Yugoslavia. Photo by Michael Lüth, with permission.

One restoration technique in peat-mined bogs in Canada has been an attempt to enhance the moisture content (Rochefort *et al*. 2002). To do this, ***Sphagnum*** (Figure 83-Figure 85) is reintroduced in the restoration areas and may be covered by extended periods of flooding, especially following snowmelt or heavy rainfall. These flooding events can cause production of **innovations** in which the buds and shoots grow. Some species grow **capitula** (compact apical branches of ***Sphagnum***) from fragments under a variety of conditions. The most species in their study grew from whole plants under long-term conditions of shallow flooding. However, many of the species under long-term flooding suffered from **etiolation** (condition of plants grown in partial or complete absence of light, characterized by long, weak stems and smaller, sparser leaves).

In the Niigata Prefecture of Japan, the floating liverwort ***Ricciocarpos natans*** (Figure 86) is common in cultivated rice fields (Shirasaki 1996). It grows best where there are warmer temperatures and a snow depth of 0.5-3.0 m.

Figure 86. ***Ricciocarpos natans*** with duckweed. Photo by Martin Hutten, with permission.

In western Norway, ***Andreaea rupestris*** (Figure 87-Figure 89) occurs along the flushing gradients created by snowmelt or is associated with snow cover (Hedger 2001). Species in the alpine areas of Norway are sensitive to the timing of snowmelt. In 43 sampled transects, 22 of the 41 taxa show a significant relationship to the time of snowmelt as the altitude increases. But these relationships are not necessarily direct responses to the temperature or water. Rather, at least some of them avoid locations of earlier snowmelt because of competition from other plants, especially tracheophytes.

Figure 87. ***Andreaea rupestris*** in the Khibiny Mountains of Russia in an area with snowmelt water and late snowbeds. Photo by Michael Lüth, with permission.

Figure 88. ***Andreaea rupestris*** with capsules, a species that grows in areas of late snowmelt. Photo by Des Callaghan, with permission.

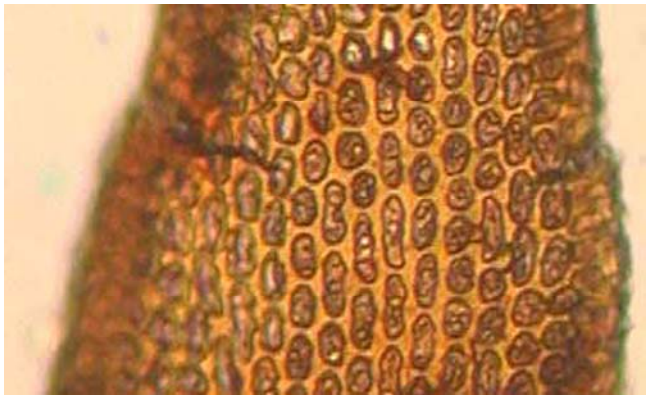

Figure 89. ***Andreaea rupestris*** leaf showing thick, pigmented cell walls that may help to protect the cell contents from cold temperatures and high UV light. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

Snowbed bryophytes must utilize low light and short growing seasons with low temperatures to attain sufficient photosynthesis for carbon gain. ***Anthelia*** (Figure 10) does especially well in the border zone of snowbeds because of its resistance to long-lasting cold, wet, and dark conditions (Lösch *et al*. 1983). ***Polytrichastrum sexangulare*** (Figure 18-Figure 20), on the other hand, is more productive and is therefore able to compete with the tracheophytes at less extreme sites.

Mechanical Effects

Snow has its down side for plants. The sheer weight can crush or break the plants. So how do tiny plants like bryophytes fare under this weight? Kennedy (1993) commented on how few studies have included the biomechanics of bryophytes, reminding us of their need for snow cover resistance.

Among the mosses receiving the greatest mechanical stress due to height is ***Dendroligotrichum dendroides*** s.l. This moss stands alone, supporting a height up to 40 cm where it lives in the forests of Chile and New Zealand. For this species, the dense hypodermal sterome provides considerable stiffness comparable to that of woody stems of tracheophytes. But for many smaller mosses, such support is usually not needed. Rather, the mosses of various habitats have a wide range of mechanical conformations. By contrast, size, development, and phylogenetic position seem to be less important than the habitat in determining growth form and mechanical adaptations.

Freeze-thaw Cycles

Free-thaw cycles can have some of the same damaging effects as dehydration-rehydration. And like many other epiphytes that tolerate the wet-dry cycles, the rock face and tree-trunk-dwelling ***Leucodon sciuroides*** (Figure 90) in the Mediterranean tolerates freezing and thawing with its photosynthetic apparatus fully operational after freezing (Deltoro *et al*. 1999). Both CO_2 fixation and chlorophyll fluorescence return to pre-freezing values during thawing. And like many desert mosses, it recovers its photosynthesis rapidly during thawing. Deltoro and coworkers suggest that this rapid recovery is possible through dissipative pathways that absorb excess light energy in frozen plants.

Figure 90. ***Leucodon sciuroides*** on tree bark, a species that tolerates freezing and is ready for photosynthesis as soon as it thaws. Photo by Michael Lüth, with permission.

Melick and Seppelt (1992) experimented with up to 16 freeze-thaw cycles in Antarctic bryophytes. After 16 days of immersion in water, there is a relatively low loss of glucose and fructose [10-29% of the total sugar pool in healthy mosses, but 69% from the dead ***Schistidium chrysoneurum*** (=***Grimmia antarctici***; Figure 91-Figure 92)]. Freeze-thaw cycles increase this leakage up to 2-3 times except in the dead mosses. ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) lost 65% of its total sugar when subjected to 16 freeze-thaw cycles. The other species [***Ceratodon purpureus*** (Figure 55-Figure 60, Figure 92), ***Schistidium chrysoneurum***, ***Cephaloziella exiliflora*** (Figure 93)] lost less than 28%. This loss does not seem to be related to the freezing temperature.

Figure 91. ***Schistidium chrysoneurum*** in the Antarctic. Photo by Rod Seppelt, with permission.

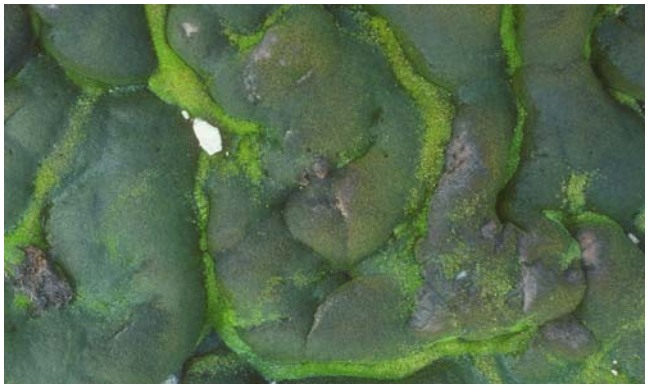

Figure 92. ***Schistidium chrysoneurum*** hummock with ***Ceratodon purpureus*** in the hollows. Photo by Rod Seppelt, with permission.

Figure 93. ***Cephaloziella*** sp. ***Cephaloziella exiliflora*** loses some of its stored sugar during freeze-thaw cycles. Photo by Kristian Peters, with permission.

Schlensog *et al*. (2004) compared the recovery of lichens and mosses after winter in the continental Antarctic. Whereas the lichens recover **photosystem II** (PS II, first protein complex in light-dependent reactions of oxygenic photosynthesis; it captures photons of light to energize electrons) almost fully within a few minutes of hydration, the mosses take much longer to recover. The moss ***Bryum subrotundifolium*** (Figure 94-Figure 96) maintains highly elevated respiration rates for several days following activation. Like the response to desiccation, it appears that this moss must repair damages before it can make a positive photosynthetic gain.

Figure 94. Bed of ***Bryum subrotundifolium*** in meltwater on Antarctica. Photo by Rod Seppelt, with permission.

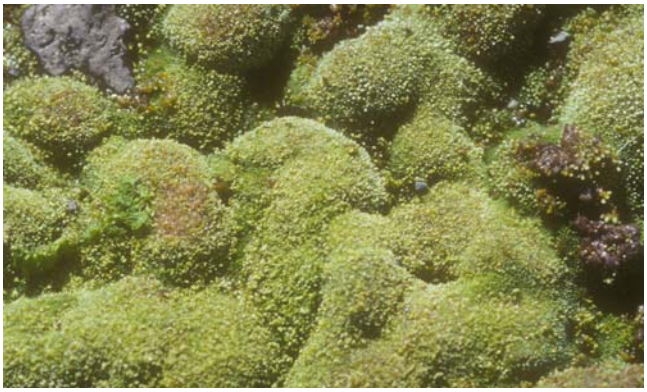

Figure 95. ***Bryum subrotundifolium***, a moss that maintains high respiration rates for several days following rehydration. Photo by Rod Seppelt, with permission.

Figure 96. ***Bryum subrotundifolium*** in the Antarctic infected with a fungus that is taking advantage of suitable moisture conditions. Photo by Catherine Beard, with permission.

Freeze-thaw protection can be conferred on bryophytes by various compounds present prior to freezing (Rütten & Santarius 1993). In ***Plagiomnium affine*** (Figure 97) the uptake and release of sucrose does little to change the permeability of the leaf cell plasma membranes to sugars, **proline** (amino acid), or polyethylene glycols. However, pretreatment with these compounds sufficient to induce plasmolysis does protect the moss cell membranes from freeze-thaw damage. On the other hand, pretreatment with **glycerol** (compound that is soluble in water and is hygroscopic) causes **plasmolysis** (shrinking of cell membrane away from cell wall) without endowing the cells with protection against freeze-thaw damage.

Figure 97. ***Plagiomnium affine***, a moss protected from freeze-thaw damage by various compounds and plasmolysis. Photo by Michael Lüth, with permission.

Winter Short-term Warming Events

Noting that climate change in northern high latitudes is likely to be greater in winter than in summer, Bjerke *et al*. (2011) examined the potential effects of more frequent short-term warming events. Whereas these warming event effects are known to be damaging to tracheophytes, their effect on bryophytes could be quite different. And the bryophytes and lichens are of major importance in these high-latitude ecosystems. By simulating winter warming events with infrared lamps and soil warming cables in a sub-Arctic heath, Bjerke *et al*. were able to monitor the responses of the feather moss ***Hylocomium splendens*** (Figure 142). In the three winters of simulated warming events, this moss experienced significant reductions in net photosynthetic rates and growth rates (of up to 48% and 52%, respectively), starting in the first summer after these events began. In this species, growth begins early in the spring season, exposing young, vulnerable shoots to the effects of cold. The researchers suggest that the damage under winter warming events may be due to breaking dormancy and experiencing premature growth during the winter warming events that causes damage to those sensitive young shoot tissues. Subsequent drying following these events may cause desiccation damage to the tender shoots.

These winter warming events could change the distribution of acrocarpous vs pleurocarpous mosses in areas with winter snow cover. In the Front Range of the Rocky Mountains, USA, Flock (1978) found that acrocarpous mosses are more abundant in areas that are dry and maintain light snow cover. Pleurocarpous mosses, on the other hand, are more abundant in wet sites with deep snow cover.

As Longton (1988) has pointed out, bryophytes in general have phenotypic plasticity, opportunistic responses in CO_2 exchange, and a poikilohydrous water relationship that endows them with considerable tolerance for desiccation and frost. These make it possible for them to occupy snowbeds where few tracheophytes can succeed.

Protection from Light Damage

A potentially serious problem for desiccated mosses at low temperatures is that they are still able to absorb light energy. This can be a special problem for forest epiphyte species that experience more light exposure in winter, compared to summer, when the tree canopy has lost its leaves. Particularly on those cold days that lack snow cover, over excitation of chlorophyll electrons can be damaging. However, Heber *et al*. (2006) report that some mosses have seasonal differences in their ability to dissipate that excess light energy into heat.

Freezing and thawing can result in photoinhibition, as demonstrated by the endemic moss ***Schistidium chrysoneurum*** (Figure 91) from the Antarctic (Lovelock *et al*. 1995a). Jägerbrand (2011) considered the time immediately following snowmelt to be the most dangerous time for UV damage to bryophytes. Rehydration, lingering low temperatures, and rising UV levels coincide with a time when bryophytes must repair the damage due to absence of light and desiccation from winter. This is especially problematic in the Antarctic where the ozone layer is thinning. Fortunately, this highly variable photoinhibition is reversible during periods of warmer temperatures (Lovelock *et al*. 1995a). The inhibition that occurs between freezing and thawing events recovers best under low light conditions. After four cycles, recovery of hydrated mosses occurred within 12 hours of transfer to 5°C at 15 μmol quanta m^{-2} s^{-1}.

During the dry summers, some desiccation-tolerant mosses are more protected against photo-oxidative damage when they are dry than they are in the humid winters (Heber *et al*. 2006). In mosses such as the **poikilohydric** (having no mechanism to prevent desiccation) ***Rhytidiadelphus squarrosus*** (Figure 98), desiccation reduction of chlorophyll fluorescence does not occur under even strong illumination in the desiccated state once the moss has achieved phototolerance. One protectant is **zeaxanthin** (one of the most common carotenoid alcohols and a powerful antioxidant), which requires drying in light. If the water is lost slowly, fluorescence is quenched. Quenchers accumulate during desiccation and remain stable until hydration occurs. Hydration results in their reversion to non-quenching molecules.

Figure 98. ***Rhytidiadelphus squarrosus***, a moss that requires drying to induce protection (zeaxanthin) against photoquenching. Photo by Michael Lüth, with permission.

Lovelock and Robinson (2002) found that surface reflective properties of leaves also plays a role in dissipating the light, hence protecting the plants from light damage. They suggested that the water content, but not pigments, of the mosses are important in altering the red-edge and photochemical reflectance index. The water content may account for the differences in reflectance among the species. All the mosses maintain high levels of xanthophyll pigments that serve as photoprotectants. Interestingly, their abilities to reflect UV light differs little. ***Bryum pseudotriquetrum*** (Figure 49-Figure 50) has greater reflective values than the other mosses studied and also has higher levels of UV-absorbing pigments, but its carotenoid levels are lower than the other species tested. ***Ceratodon purpureus*** (Figure 55-Figure 60) has higher levels of anthocyanins but lower total chlorophyll concentrations. ***Bryum pseudotriquetrum*** has higher levels of the specific UV-screening pigments; ***Ceratodon purpureus*** and ***Schistidium chrysoneurum*** (Figure 91) have higher levels of pigments that protect against excess visible light.

For ***Schistidium chrysoneurum*** (Figure 91), freezing in darkness reduced the $\mathbf{F_v/F_m}$ **ratio** (ratio of variable:maximum fluorescence) and the initial fluorescence (Lovelock *et al*. 1995b). These were reversible when the mosses thawed. The reduction of F_v/F_m may be the result of conformational changes in the pigment-protein complexes due to the desiccation that occurs during freezing. The photoinhibition during freezing is reversible and indicates that processes that protect the moss from photoinhibitory damage during freezing temperatures occur in consort with high solar radiation levels. These protections therefore limit the repair needed when favorable temperatures return.

Winter Growth

Proctor (2000) points out that bryophytes have a desiccation tolerance strategy that differs from that of tracheophytes. Bryophytes are able to survive because they can photosynthesize and grow when water is freely available, then suspend their metabolism when it is not. By being **ectohydric** (conducting water externally), many species can have wide variability in their external capillary water without affecting the water content of the cells. This external source permits the cells to function most of the time with full turgor. When they do desiccate, the period of water stress is brief. They have a carbohydrate content that is similar to that of the maturing embryos of desiccation-tolerant seeds. It is likely that these carbohydrates contribute to their rapid recovery upon rehydration. In short, they mimic temperate winter annuals or mesic desert ephemerals. For example, in the maritime climate of Britain, the wall top moss ***Grimmia pulvinata*** (Figure 99) takes advantage of the mild climate of autumn and early winter for most of its growth (Proctor 2004). During that period the moss is able to maintain hydration for long periods of time to carry out photosynthesis. Like many mosses, it is adapted to frequent and often short wet-dry cycles.

Figure 99. ***Grimmia pulvinata*** on rock where it grows mostly in autumn an dearly linter when it is well hydrated frequently. Photo by Michael Lüth, with permission.

Even growth rates seem to adjust to differences in temperature, perhaps because of differences in available moisture, perhaps just to acclimation (see Fornwall & Glime 1982). For example, ***Brachythecium rutabulum*** (Figure 100) has superior growth in winter compared to summer when grown at temperatures below 18°C (Furness & Grime 1982). Most species of temperate regions seem to have their optimum growth temperature at 15-25°C, but growth can be extensive at temperatures even below 10°C. Gaberščik and Martinčič (1987) demonstrated seasonal changes in growth of ***Sphagnum papillosum*** (Figure 83-Figure 85) in a raised bog in Slovenia, Yugoslavia. They found the greatest growth at the beginning of the growing

season, a time when water is usually plentiful. During winter months, the photosynthetic activity declined and ceased completely in February.

Figure 100. ***Brachythecium rutabulum*** on Populus x canadensis log, emerging from the snow. Photo by Pim Rijkee, through Wikimedia Commons.

Asada *et al*. (2003) found that winter growth of a number of bryophyte species [***Racomitrium lanuginosum*** (Figure 101-Figure 103), ***Pleurozium schreberi*** (Figure 104), ***Sphagnum austinii*** (Figure 105-Figure 106), ***S. fuscum*** (Figure 2), ***S. rubellum*** (Figure 107-Figure 108), ***S. papillosum*** (Figure 83-Figure 85), ***S. lindbergii*** (Figure 38-Figure 39), ***S. tenellum*** (Figure 109-Figure 110), ***S. pacificum*** (Figure 111)] in a coastal peatland in British Columbia, Canada, is an important contribution to the productivity of the system. But for this productivity to occur, water must be available during those times when the temperature permits photosynthesis to occur. Asada further supported the importance of water by demonstrating that productivity in these species correlated more strongly with precipitation than with temperature.

Figure 101. ***Racomitrium lanuginosum*** forming massive hummocks in Iceland. Photo by Janice Glime.

Figure 102. ***Racomitrium lanuginosum*** forming hummocks that benefit from late season snowmelt water. Photo by Michael Lüth, with permission.

Figure 103. ***Racomitrium lanuginosum***, a species that has winter growth in coastal wetlands. Photo by Juan Larrain, with permission.

Figure 104. ***Pleurozium schreberi***, a moss that can tolerate frequent wet-dry cycles and grows best in the seasons with the best hydration. Photo by Janice Glime.

Figure 105. ***Sphagnum austinii*** wetland habitat. Photo by Michael Lüth, with permission.

Figure 106. ***Sphagnum austinii*** with a sundew that shares its habitat. Photo by Michael Lüth, with permission.

Figure 107. ***Sphagnum rubellum*** wetland habitat. Photo by Michael Lüth, with permission.

Figure 108. ***Sphagnum rubellum***, a species that benefits fro winter growth in coastal peatlands. Photo by Michael Lüth, with permission.

Figure 109. ***Sphagnum tenellum*** showing its very wet habitat that permits it to take advantage of late season photosynthesis. Photo by Michael Lüth, with permission.

Figure 110. ***Sphagnum tenellum***, a moss that can benefit from winter photosynthesis. Photo by Michael Lüth, with permission.

Figure 111. ***Sphagnum pacificum***, a moss that takes advantage of late season photosynthesis. Photo by Vita Plasek, with permission.

Growth can actually occur at sub-zero temperatures. ***Brachythecium geheebii*** (Figure 112) and ***Homalothecium philippeanum*** (Figure 113-Figure 114) in Romania montane areas are able to assimilate CO_2 down to -9°C (Atanasiu 1971). ***Isothecium alopecuroides*** (Figure 115-Figure 116) had net gain down to about -8°C. Both of these temperatures are lower than those for evergreen trees tested in winter. But not all bryophytes are created equal. Davey and Rothery (1996) found that in ***Brachythecium austrosalebrosum*** from the Antarctic, respiration rates were highest in summer and lowest in winter regardless of temperature within the natural range, but that in ***Chorisodontium aciphyllum*** (Figure 117-Figure 118) and ***Andreaea depressinervis*** (Figure 119), there was little change with season.

Figure 112. ***Brachythecium geheebii***, a species that can have net photosynthetic gain down to -9°C. Photo by Michael Lüth, with permission.

Figure 113. ***Homalothecium philippeanum*** in a habitat where it can be exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.

Figure 114. ***Homalothecium philippeanum*** on a boulder where it can photosynthesize when the air temperature is as low as -9°C. Photo by Michael Lüth, with permission.

Figure 115. ***Isothecium alopecuroides*** growing epiphytically where it is exposed to sub-zero temperatures. Photo by Michael Lüth, with permission.

Figure 116. ***Isothecium alopecuroides***, a species that has photosynthesis down to -8°C. Photo by David Holyoak, with permission.

Figure 117. ***Chorisodontium aciphyllum*** in Antarctica where its respiration differs little with seasons. Photo from Polar Institute, through Creative Commons.

Figure 118. ***Chorisodontium aciphyllum***, a moss whose respiration differs little with season. Photo by Juan Larrain, with permission.

Figure 119. ***Andreaea depressinervis***, an Antarctic species whose respiration differs little with season. Photo from Wikimedia Commons.

A recent addition to the known flora of the British Isles, the thallose liverwort ***Athalamia hyalina*** (Figure 120) is a Northern Hemisphere montane species (Long *et al*. 2003). In Scotland it has its active growth in the winter and produces its spores in spring. This permits it to live on the thin soil of eroding limestone ledges where it can take advantage of the moisture in fog of winter and intermittent thaws.

Figure 120. ***Athalamia hyalina***, a liverwort that grows in winter in Scotland. Photo by Michael Lüth, with permission.

Winter warming (and possibly summer drought?) in the UK seems to account for the increases in ***Campyliadelphus chrysophyllus*** (Figure 121) and ***Fissidens dubius*** (Figure 122) in a limestone grassland, as demonstrated with experiments in winter warming and increased supplemental rainfall in summer (Bates 2006). Spread of the epiphytes ***Cololejeunea minutissima*** (Figure 123) and ***Colura calyptrifolia*** (Figure 124) seems likewise to be the result of rising temperatures in winter, and possibly a change in the summer moisture. On the other hand, winter warming coincides with decreases in ***Rhytidiadelphus squarrosus*** (Figure 98) and ***Lophocolea bidentata*** (Figure 125).

Figure 121. ***Campyliadelphus chrysophyllus***, a species that is increasing in abundance in the UK as a result of winter warming. Photo by David Holyoak, with permission.

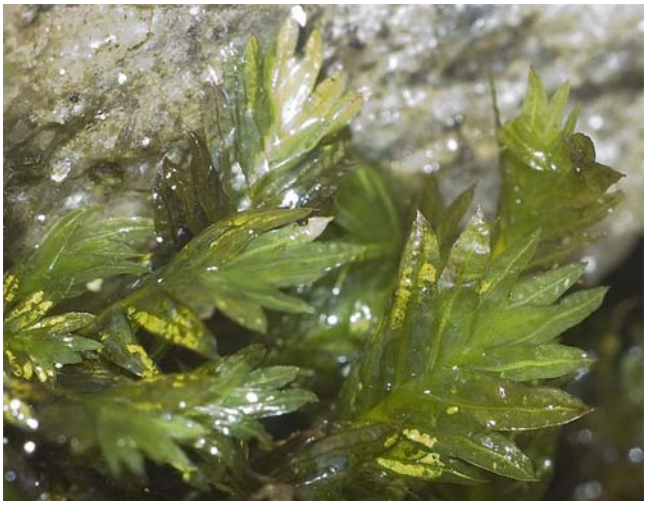

Figure 122. ***Fissidens dubius***, a species that is increasing in abundance in the UK as a result of winter warming. Photo by Aimon Niklasson, with permission.

Figure 123. ***Cololejeunea minutissima*** on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by David T. Holyoak, with permission.

Figure 124. ***Colura calyptrifolia*** on bark, a species that seems to be spreading in the UK concomitant with rising mean winter temperatures. Photo by Michael Lüth, with permission.

Figure 125. ***Lophocolea bidentata***, a species that seems to be disappearing from the UK due to winter warming. Photo by Michael Lüth, with permission.

Winter and Reproduction

Since winter is often the season with moisture in some habitats like deserts, we can expect this to be the season of gamete transfer and fertilization. In the Negev Desert of southern Israel, Herrnstadt and Kidron (2005) found that ***Bryum dunense*** initiates its reproductive organs prior to the first winter rain, using atmospheric humidity from dew and fog as the source of water. The most sporophytes form in the partially shaded microhabitats following winter rains, interestingly exceeding those in the shaded microhabitats. When the first rain arrives, ***B. dunense*** is ready to disperse its bulbils and to complete fertilization. The shrubs seem to be essential to provide the partial shade in which this species is most successful at reproducing.

Too little rainfall in winter can be detrimental to desert mosses. ***Syntrichia inermis*** (Figure 126) in the Mojave Desert, Nevada, USA, failed to initiate sporophytes in 1996 and 1997 when the winter-spring rainfall was reduced (Stark 2001). In ***Crossidium crassinerve*** (Figure 127), the appropriate hydration periods occurred in the cooler months of October to April (Stark 2005). Hydration in the summer was detrimental because the patches dried too quickly (as few as 3 hours) following the rainfall, prohibiting sufficient repair and carbon gain. During the four years of the study, the five patches monitored initiated 248 sporophytes; only 9 survived. Embryonic abortion (69%) and capsule herbivory (30%) accounted for most of the deaths.

Acaulon triquetrum (Figure 128) in southwest Germany initiates most of its gametangia in October to December (Ahrens 2003). These develop rapidly, permitting fertilization to occur during the same time period. Sporophytes grow in October-November to January-February, with dispersal in April or May. The **chloronemal** (branches of protonemata that give rise to gametophore buds) filaments are persistent through summer but die off during winter (December – February). The rhizoid system, however, persists throughout the winter, once again giving rise to new chloronemata and gametophores in the spring. Having rhizoids that persist through the winter permits this moss to rapidly occupy bare surfaces, especially the loess created by small, burrowing mammals.

Figure 126. ***Syntrichia inermis*** dry, a species that frequently fails to produce sporophytes due to insufficient rainfall in winter and spring in the Mojave Desert, USA. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 127. ***Crossidium crassinerve***, a species that is hydrated mostly in winter and early spring in the Mojave Desert. Photo by Michael Lüth, with permission.

Figure 128. ***Acaulon triquetrum***, a species that initiates its gametangia October-December in Germany. Photo by Michael Lüth, with permission.

Laaka-Lindberg and Heino (2001) found that the leafy liverwort ***Lophozia ventricosa*** (var. ***silvicola***; Figure 129) in southern Finland has two types of gemmae. One of these becomes dormant and the other is non-dormant. Only the dormant gemmae are able to survive the winter. She provided the evolutionary argument that if the winter mortality (of non-dormant gemmae) increases compared to the mortality during the growing season, then evolution would favor an increase in the percentage of dormant gemmae, especially among those produced at the end of the growing season.

Figure 129. ***Lophozia ventricosa*** with gemmae. This species produces two types of gemmae, one of which survives winter. Photo by Jan-Peter Frahm, with permission.

Spore dormancy is also subject to temperature. Spores require water to germinate, but dormancy loss also occurs in response to temperature. For ***Sphaerocarpos texanus*** (Figure 130) at 35/20°C, loss of spore dormancy increases faster than that in even modestly lower temperatures of 30/15°C or 25/15°C (McLetchie 1999). The best spore germination occurs at 16/10°C and spores fail to germinate at 35/20 or 30/15°C. But low temperatures induce the spores to return to dormancy. McLetchie considered this behavior to be similar to that of seeds of obligate winter annuals.

Figure 130. ***Sphaerocarpos texanus***, a species that loses its spore dormancy at higher temperatures. Photo by Martin Hutten, with permission.

Longton and Greene (1969) demonstrated that in Britain the boreal forest moss ***Pleurozium schreberi*** (Figure 104) sustains survival of its antheridia through winter. The antheridia begin development in August but remain immature through winter. The archegonia likewise overwinter in an immature stage. When spring arrives, both undergo rapid development, preparing them for fertilization in April and May. The sporophyte matures in autumn and spores are dispersed between January and April.

It is likely that the moss ***Dichelyma japonicum*** is excluded from high altitudes and latitudes because its sporophytes have a late sporophyte maturation (Shirasaki 1997). This species grows on the woody plants beside ponds and streams and is covered by deep snow in winter. In the aquatic family **Fontinalaceae**, this species requires deep snow in winter and high precipitation in summer.

Riccia cavernosa (Figure 131) avoids most of the problems of cold, dark, dry winters by having an extremely short life cycle on the banks and sandy flats of the Kobuk River in Alaska (Seppelt & Laursen 1999). Its spore to spore cycle is only three to four weeks of late summer and autumn! Hence, it is able to overwinter as spores and avoid all the problems. On the other hand, this same species (perhaps a different race?) has a life cycle of two - three months of winter and early spring in Australia.

Figure 131. ***Riccia cavernosa***, a species with a 3-4-week life cycle in Alaska and one of 2-3 months in Australia. Photo from <www.aphotofauna.com>, with permission.

Hennediella heimii (Figure 132) holds the record for the most polar sporophytes. Seppelt *et al*. (1992) reported this species with young sporophytes from the Lower Taylor Valley, Victoria Land, Antarctica (77°55'S).

Figure 132. ***Hennediella heimii*** with capsules; this species has the record for capsules at the highest latitude in the Antarctic. Photo by Michael Lüth, with permission.

Asexual Survival

We have learned much about preparation for winter conditions through studies in cryopreservation. The pioneer moss ***Ditrichum plumbicola*** (Figure 133) survives winters and desiccation in the field, but has poor survival of cryopreservation, even with pretreatment (Rowntree *et al*. 2007). Using a series of treatments and observations, Rowntree and co-workers attempted to determine the effects of ABA, sucrose, and desiccation on various stages of the protonemata. What they found was that most of the protonemal cells pretreated with ABA and sucrose died, but the ones that survived had thick cell walls with deep pigmentation, numerous small vacuoles, and cytoplasmic lipid droplets. Those with only desiccation and cryopreservation exhibited little cytological change. Removal of the ABA-sucrose pretreatment permitted normal development and activity of the protonemata, whereas the pretreatment induced propagules from the protonemata, and these propagules were highly desiccation tolerant and easily survived the cryopreservation. In nature, this species forms highly desiccation-tolerant rhizoids that serve the same perennating function.

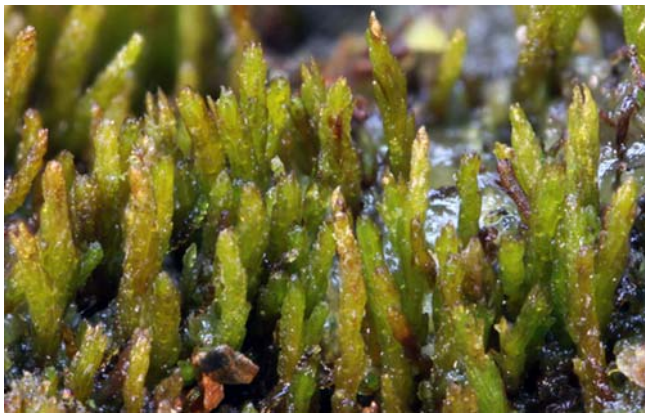

Figure 133. ***Ditrichum plumbicola***, a species that survives winter and desiccation in the field, but it has little ability to survive cryopreservation except as propagules. Photo by Des Callaghan, with permission.

Sympatric Differences

Seasonal differences in reproduction often separate **sympatric** (two species that exist in same geographic area) species and keep them separated reproductively. Such is the case for three species of ***Dicranoloma*** in Australia (Milne 2001). In ***D. menziesii*** (Figure 134) and ***D. platycaulon*** (Figure 135), the antheridia are initiated during winter and archegonia in the following spring, whereas in ***D. billardierei*** (Figure 136) the antheridia initiate during late spring to summer whereas archegonia originate in autumn. Differences in development time place the times of fertilization in three different time periods, late summer for ***D. menziesii***, mid autumn for ***D. platycaulon***, and early winter for ***D. billardierei***. For all three species, the winter season is an important period for this process, providing sufficient moisture and avoiding these activities during the high summer temperatures that can cause excessive respiration.

Figure 134. ***Dicranoloma menziesii***, a species separated from its congeners by its reproductive times. Photo by Andrew Hodgson, with permission.

Figure 135. ***Dicranoloma platycaulon***, a species separated from its congeners by its reproductive time. Photo by David Tng, with permission.

Figure 136. ***Dicranoloma billardierei***, a species separated from its congeners by its reproductive times. Photo by Michael Lüth, with permission.

In Japan, ***Trachycystis flagellaris*** (Figure 137) has developing sporophytes that do well in the lower temperatures and deep snow at higher altitudes (Shirasaki 1998). ***Trachycystis microphylla*** (Figure 138), on the other hand, has its sporophyte maturation in early spring; it seems to be restricted to coastal areas with only thin snow cover in winter.

Figure 137. ***Trachycystis flagellaris***, a species whose developing sporophytes survive well under deep snow. Photo by Ivanov, with permission.

Figure 138. ***Trachycystis microphylla***, a species that can survive only a thin snow cover. Photo by Li Zhang, with permission.

Effects of Bryophytes on their Communities in Winter

We cannot ignore the importance of the perennial nature of most bryophytes. Many remain active in winter, but even more importantly they are present and active within hours of snowmelt on their leaves.

The ability of the mosses to remain green and moist throughout winter in some areas is important for their invertebrate inhabitants. For example, in the Black Forest of Germany, ***Rhytidiadelphus squarrosus*** (Figure 98) is home to several species of tardigrades (water bears) (Schuster & Greven 2007). These tiny animals are well attuned to the seasonal changes in moss habitats. Their diversity is greatest in winter, although numbers decline then. (See Volume 2, Chapter 5).

Mosses are able to modify the effects of frost on the soil community. In a feather moss community in northwestern Alberta, Canada, dominated by ***Pleurozium schreberi*** (Figure 104), removal of the moss layer increased soil temperatures in summer and lengthened the frost-free period (Startsev *et al*. 2007). But rather than causing the soil to be warmer, the bare soil had temperatures as low as -13°C during the frost-free times.

In China, mosses are a critical part of the gall nut industry, a valuable source of medicines and chemicals. The gall aphid, ***Kaburagia rhusicola*** spends its winters on mosses, including ***Brachythecium*** spp., ***Entodon***, and ***Oxyrrhynchium*** (Lai & Zhang 1994). The mosses are able to provide both cover and a moist location. The gall aphid ***Kaburagia ovogallis*** uses eight species of the **Brachytheciaceae** for its winter hosts (Li 1990). In fact, as of 1990, 24 species of mosses were identified as winter hosts of various species of gall aphids. By providing more of these mosses, those in the gall nut industry were able to sustain higher yields.

Lichens (especially reindeer "moss") are well known as food for caribou and other large herbivores in winter. But bryophytes are less well known for this role. Oloffson *et al*. (2002) demonstrated the importance of bryophytes and other food sources by using exclosures around parts of snowbeds in Arctic-alpine tundra communities. Following eleven years of exclosure, the snowbed developed significant increase in both tracheophytes and bryophytes. The same response did not occur in the tall herb meadow. The primary herbivores in the study were rodents – grey-sided voles (***Clethrionomys rufocanus***), red voles (***C. rutilus***), field voles (***Microtus agrestis***), root voles (***M. oeconomus***), and lemmings (***Lemmus lemmus***). Bryophytes accounted for most of the cryptogamic changes in biomass. Predominant among those increasing in biomass were ***Sanionia uncinata*** (Figure 46-Figure 48) (584% increase) and ***Polytrichum juniperinum*** (Figure 139) (113,584% increase). ***Pleurozium schreberi*** (Figure 104) was absent in the controls and increased by 2.7g m^{-2} in the exclosures. The researchers concluded that the low competition of the unproductive snowbeds was caused by these mammalian herbivores that depressed the plant biomass. The presence of food under the snow, including the bryophytes, permits these animals to remain hidden from aerial predators.

Figure 140. ***Polytrichum juniperinum***, a species that increases in biomass following grazing by rodents in the Arctic. Photo by Michael Lüth, with permission.

Prins (1982) asked why mosses are eaten in cold climates only. Could it be that they like the sweet taste of sucrose that is stored in some species in preparation for winter?

Winter Dispersal

Winter can be a time for dispersal. Dry, brittle mosses easily break, presenting fragments that can travel long distances across the smooth snow or caught up in winds unimpeded by canopy leaves. McDaniel and Miller (2000) demonstrated this by collecting bryophyte fragments from late-spring snowbeds in the Adirondack Mountains, New York, USA. The diversity of fragments from the higher elevations of alpine and krummholz vegetation was much greater than that in the forested site. (The diversity also surpassed that of the tracheophytes.)

Miller and Howe Ambrose (1976) were able to collect bryophyte fragments from late snowbeds on Bathurst Island in the Canadian high Arctic. These collections contained large numbers of both mosses and liverworts. Most of the species represented those on the nearby ridges and slopes and Miller and Howe Ambrose presumed that these had been dispersed during the previous winter, resulting from surface winds. In lab cultures, 12% of these fragments exhibited viability, producing protonemata, new shoots, rhizoids, or renewed growth. But parts were not equally viable. Detached moss leaves did not grow and only one leafy liverwort fragment was viable. Rather, the leafy gametophore tips were the most successful. Nevertheless, the researchers estimated that a cubic meter of granular snow contained more than 4000 viable propagules!

Pollution Effects – Vital Water or Deadly Poisons?

Kennedy (1993) reminded us that traditional wisdom tells us that life in the Antarctic is restricted by the arrival of new species and the extreme cold. But recently biogeographical evidence indicates that water may be the primary limiting factor. But it can also bring danger.

Winter can be a particularly dangerous time for bryophytes that are subject to air pollution. The snow collects the pollutants over the extended period of snow cover (Thomas 1981). When melting occurs, the bryophytes are subjected to that long-term collection of pollutants, *i.e.*, concentrated pollutants, in what is known as **acid flush** (Woolgrove & Woodin 1996). Woolgrove and Woodin documented that these concentrated pollutants in the snowbed moss ***Kiaeria starkei*** are causing damage to the underlying bryophytes. This damage is greatest when the snow cover is gone and meltwater is delivered to the active plants. This exposure can last for a sufficient period of time that no recovery is measured after 4 weeks. This, combined with the short growing season of these mosses in snowbeds, can have serious impacts on their survival.

Markert and Weckert (1993) found that plants of ***Polytrichastrum formosum*** (Figure 141) had the maximum concentrations of pollutants in winter and the lowest in summer, attributing this to the higher biomass productivity of this species in the spring. But I suspect that part of this effect was due to the accumulation effect by the snow. Hynninen (1986) attributed the greater winter accumulation of heavy metals by ***Sphagnum*** (Figure 83-Figure 85) in moss bags in Finland to the summer holiday breaks. Could these winter highs be due to the absence of rain to wash the pollutants away and the long time for continuous collection?

In the boreal forest ***Hylocomium splendens*** (Figure 142) uses both organic and inorganic nitrogen deposited in the snow (Forsum *et al*. 2008). Snowmelt N is dominated by nitrates (86%), followed by ammonia (11%) and amino acids (3%). The ***H. splendens*** is able to take up 24% of the nitrogen from the snow nitrogen. On the other hand, Björk (2007) showed that 1.0 g m^{-2} yr^{-1} N added to the snow water had little effect on the bryophyte community over a three-year period. Other nutrients become available in the snowmelt water as well (Björk & Molau 2007; Jägerbrand 2011).

Figure 141. ***Polytrichastrum formosum*** with capsules, a species that accumulates the most pollutants in winter. Photo by David T. Holyoak, with permission.

Like growth, uptake of pollutants depends on the availability of water, and it may or may not be significantly affected by temperature. As concluded by Hébrard *et al*. (1974) for ***Grimmia orbicularis*** (Figure 143), the activities of ^{90}Sr transfer to the mosses coincide with those times of maximum rainfall in autumn, winter, and spring. The accumulations of the pollutant in dust on the moss is unavailable to the moss until water enters the cells.

Figure 142. ***Hylocomium splendens***, a species that takes a great deal of its nitrogen from snowmelt. Photo by Chmee, through Creative Commons.

Figure 143. ***Grimmia orbicularis***, a species that collects pollutants that are detrimental to it when it rains. Photo by Michael Lüth, with permission.

Summary

Late snowbeds provide a refuge for bryophytes where there is sufficient water in "spring" and reduced competition from tracheophytes. Species living there have life cycles that take advantage of snowmelt water and that have life cycle stages that can live through winter. The growth forms may be altered and duration of the snow is a determining factor in species composition. Prominent among the snowbed bryophytes are species of ***Anthelia*** and ***Kiaeria***. Snowmelt waters create flushes that have their own species, including several ***Sphagnum*** species.

Freeze-thaw cycles can be beneficial to some and detrimental to other bryophytes. Short thaw periods may be insufficient to repair damage from desiccation and freezing. These can become lethal for some bryophytes that are unable to realize any carbon gain. In some locations, especially the Antarctic, exposure in winter subjects the bryophytes to higher UV light intensities, coupled with low temperatures. Some live in exposed sites where wind clears the snow or on vertical surfaces that do not hold the snow, exposing the bryophytes to drying, intense light, and extreme low temperatures.

On the other hand, some bryophytes grow best in winter when more moisture is available. Others survive winter through asexual propagules. The life cycle adaptations to winter microclimate are effective means for maintaining species differences among sympatric members of the same genus.

Bryophytes occupy habitats where tracheophytes cannot complete their life cycles in the short growing seasons. These bryophytes provide a refuge and food for invertebrates, rodents, and even some large free-range mammals. They modulate the ground temperature, preventing extremes, hold water longer than bare ground, and prevent destructive runoff during spring flushes.

The dry air of winter facilitates breakage of bryophyte fragments. These easily blow across the snow, taking advantage of the absence of leaves on the trees in deciduous forests, making winter dispersal significant.

Pollutants accumulate in the snow and rapid melt may expose the bryophytes to heavy concentrations in a short time frame. In some cases, the bryophytes gain important nutrients from the collected pollutants, but some are detrimental.

Acknowledgments

Thank you to all the photographers who kindly gave permission for use of their photos. Omar Pokorni was kind enough to tell me the link to this chapter was not working.

Literature Cited

Ahrens, M. 2003. The phenology and life history of *Acaulon triquetrum* (Bryopsida, Pottiaceae). Herzogia 16: 239-274.

Asada, T., Warner, B. G., and Banner, A. 2003. Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. Bryologist 106: 516-527.

Atanasiu, L. 1971. Photosynthesis and respiration of three mosses at winter low temperatures. Bryologist 74: 23-27.

Bailey, J. W. 1933. Mosses found near summer snowbanks. Bryologist 36: 8-11.

Bates, J. 2006. Effects of simulated climatic changes on the bryophytes of a limestone grassland. Field Bryol. 89: 12-13.

Belland, R. J. 1983. A late snowbed bryophyte community in western Newfoundland, Canada. Can. J. Bot. 61: 218-223.

Bjerke, J. W., Bokhorst, S., Zielke, M., Callaghan, T. V., Bowles, F. W., and Phoenix, G. K. 2011. Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. J. Ecol. 99: 1481-1488.

Björk, R. G. 2007. Snowbed Biocomplexity: A Journey from Community to Landscape. Göteborg University, Göteborg.

Björk, R. G. and Molau, U. 2007. Ecology of alpine snowbeds and the impact of global change. Arct. Antarct. Alp. Res. 39: 34-43.

Davey, M. C. and Rothery, P. 1996. Seasonal variation in respiratory and photosynthetic parameters in three mosses from the maritime Antarctic. Ann. Bot. 78: 719-728.

Deltoro, V. I., Calatayud, A., Morales, F., Abadía, A., and Barreno, E. 1999. Changes in net photosynthesis,

chlorophyll fluorescence and xanthophyll cycle interconversions during freeze-thaw cycles in the Mediterranean moss *Leucodon sciuroides*. Oecologia 120: 499-505.

Dorrepaal, E., Aerts, R., Cornelissen, J. H. C., Callaghan, T. V., and Logtestijn, R. S. P. van. 2004. Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. Global Change Biol. 10(1): 93-104.

Flock, J. W. 1978. Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. Arct. Alp. Res. 10: 31-47.

Fornwall, M. D. and Glime, J. M. 1982. Cold and warm-adapted phases in *Fontinalis duriaei* Schimp. as evidenced by new assimilatory and respiratory responses to temperature. Aquatic Botany 13: 165-177.

Forsum, Å, Laudon, H., and Nordin, A. 2008. Nitrogen uptake by *Hylocomium splendens* during snowmelt in a boreal forest. Ecoscience 15: 315-319.

Frenzke, L., Wanke, S., Isnard, S., Stoll, A., Neinhuis, C., Rowe, N. P. 2011. Stem biomechanics of the giant moss *Dendroligotrichum dendroides* s.l. and its significance for growth form diversity in mosses. J. Bryol. 33: 229-236.

Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes II. A comparative study of species of contrasted ecology. J. Ecol. 70: 525-536.

Gaberščik, A. and Martinčič, A. 1987. Seasonal dynamics of net photosynthesis and productivity of *Sphagnum papillosum*. Lindbergia 13: 105-110.

Heber, U., Bilger, W., and Shuvalov, V. A. 2006. Thermal energy dissipation in reaction centres and in the antenna of photosystem II protects desiccated poikilohydric mosses against photo-oxidation. J. Exper. Bot. 57: 2993-3006.

Hébrard, J.-P., Foulquier, L., and Grauby, A. 1974. Appro che experimentale sur les possibilites de transfert du ^{90}Sr d'un substrat solide a une mousse terrestre: *Grimmia orbicularis* Bruch. Bull. Soc. Bot. France 121: 235-250.

Hedger, E. 2001. Environmental relationships of perichaetial and sporophyte production in *Andreaea* spp. in western Norway. J. Bryol. 23: 97-108.

Herrnstadt, I. and Kidron, G. J. 2005. Reproductive strategies of *Bryum dunense* in three microhabitats in the Negev Desert. Bryologist 108: 101-109.

Horikawa, Y. and Ando, H. 1963. A review of the Antarctic species of *Ceratodon* described by Cardot. Hikobia 3: 275-280.

Hynninen, V. 1986. Monitoring of airborne metal pollution with moss bags near an industrial source at Harjavalta, southwest Finland. Ann. Bot. Fenn. 23: 83-90.

Jägerbrand, A. K. 2011. Effects of climate change on tundra bryophytes. In: Tuba, Z., Slack, N. G., and Stark, L. R. Bryophyte Ecology and Climate Change. Cambridge University Press, Cambridge, pp. 211-236.

John, E. A. 1990. Fine scale patterning of species distributions in a saxicolous lichen community at Jonas Rockslide, Canadian Rocky Mountains. Holarct. Ecol. 13: 187-194.

Kaiser, G. B. 1921. Little journeys into mossland, II.--A February thaw. Bryologist 24: 5-6.

Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. Arct. Alp. Res. 125: 308-315.

Laaka-Lindberg, S. and Heino, M. 2001. Clonal dynamics and evolution of dormancy in the leafy hepatic *Lophozia silvicola*. Oikos 94: 525-532.

Li, X.-J. 1990. Study on the winter host mosses of gall aphids from China. In: Koponen, T. (ed.). Congress of East Asiatic Bryology, Helsinki. Programme and Abstracts, p. 26.

Long, D. G., Rothero, G. P., and Paton, J. A. 2003. *Athalamia hyalina* (Sommerf.) S. Hatt. in Scotland, new to the British Isles. J. Bryol. 25: 253-257.

Longton, R. E. 1981. Inter-populational variation in morphology and physiology in the cosmopolitan moss *Bryum argenteum* Hedw. J. Bryol. 11: 501-520.

Longton, R. E. 1988. Adaptations and strategies of polar bryophytes. Bot. J. Linn. Soc. 98: 253-268.

Longton, R. E. and Greene, S. W. 1969. The growth and reproductive cycle of *Pleurozium schreberi* (Brid.) Mitt. Ann. Bot. N. S. 33: 83-105.

Lösch, R., Kappen, L., and Wolf, A. 1983. Productivity and temperature biology of two snowbed bryophytes. Polar Biol. 1: 243-248.

Lovelock, C. E. and Robinson, S. A. 2002. Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. Plant Cell Environ. 25: 1239-1250.

Lovelock, C. E., Osmond, C. B., and Seppelt, R. D. 1995a. Photoinhibition in the Antarctic moss *Grimmia antarctici* Card when exposed to cycles of freezing and thawing. Plant Cell Environ. 18: 1295-1402.

Lovelock, C. E., Jackson, A. E., Melick, D. R., and Seppelt, R. D. 1995b. Reversible photoinhibition in Antarctic moss during freezing and thawing. Plant Physiol. 109: 955-961.

Markert, B. and Weckert, V. 1993. Time-and-site integrated long-term biomonitoring of chemical elements by means of mosses. Toxicol. Environ. Chem. 40(1-4): 43-56.

McDaniel, S. F. and Miller, N. G. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. Bryologist 103: 592-600.

McLetchie, D. N. 1999. Dormancy/nondormancy cycles in spores of the liverwort *Sphaerocarpos texanus*. Bryologist 102: 15-21.

Melick, D. R. and Seppelt, R. D. 1992. Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. Antarct. Sci. 4: 399-404.

Melick, D. R., Hovenden, M. J., and Seppelt, R. D. 1994. Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, Continental Antarctica. Vegetatio 111: 71-87.

Miller, N. G. 1989. Late-Pleistocene *Anthelia* (Hepaticae), an arctic-alpine, snow-bed indicator at a low elevation site in Massachusetts, U. S. A. J. Bryol. 15: 583-588.

Miller, N. G. and Howe Ambrose, L. J. 1976. Growth in culture of wind-blown bryophyte gametophyte fragments from Arctic Canada. Bryologist 79: 55-63.

Milne, J. 2001. Reproductive biology of three Australian species of *Dicranoloma* (Bryopsida, Dicranaceae): Sexual reproduction and phenology. Bryologist 104: 440-452.

Mulder, C. P. H., Uliassi, D. D., and Doak, D. F. 2001. Physical stress and diversity-productivity relationships: The role of positive interactions. Proc. Natl. Acad. Sci. USA 98: 6704-6708.

Oloffson, J., Moen, J., and Oksanen, L. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. Oikos 96: 265-272.

Pannewitz, S., Schlensog, M., Green, T. G. A., Sancho, L. G., and Schroeter, B. 2003. Are lichens active under snow in continental Antarctica? Oecologia 135: 30-38.

Priddle, J. 1979. Morphology and adaptation of aquatic mosses in an Antarctic lake. J. Bryol. 10: 517-529.

Prins, H. H. T. 1982. Why are mosses eaten in cold environments only? Oikos 38: 374-380.

Proctor, M. C. 2000. The bryophyte paradox: Tolerance of desiccation, evasion of drought. Plant Ecol. 151: 41-49.

Proctor, M. C. F. 2004. How long must a desiccation-tolerant moss tolerate desiccation? Some results of two years' data logging on *Grimmia pulvinata*. Physiol. Plant. 122: 21-27.

Rochefort, L., Campeau, S., and Bugnon, J.-L. 2002. Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*? Aquat. Bot. 74: 327-341.

Rothero, G. 2007. Saying goodbye to our Arctic? The future of snowbed vegetation in Scotland. Field Bryol. 91: 40-41.

Rowntree, J. K., Duckett, J. G., Mortimer, C. L., Ramsay, M. M., and Pressel, S. 2007. Formation of specialized propagules resistant to desiccation and cryopreservation in the threatened moss *Ditrichum plumbicola* (Ditrichales, Bryopsida). Ann. Bot. 100: 483-496.

Rütten, D. and Santarius, K. A. 1993. Cryoprotection of *Plagiomnium affine* induced by various natural and artificial substances. Can. J. Bot. 71: 793-798.

Schlensog, M., Pannewitz, S., Green, T. G. A., and Schroeter, B. 2004. Metabolic recovery of continental Antarctic cryptogams after winter. Polar Biol. 27: 399-408.

Schuster, R. and Greven, H. 2007. A long-term study of population dynamics of tardigrades in the moss *Rhytidiadelphus squarrosus* (Hedw.) Warnst. J. Limnol. 66(Suppl. 1): 141-151.

Seppelt, R. D. and Laursen, G. A. 1999. *Riccia cavernosa* Hoffm. emend Raddi, new to the Arctic and the bryoflora of Alaska. Hikobia 13: 71-76.

Seppelt, R. D. and Selkirk, P. M. 1984. Effects of submersion on morphology and the implications of induced environmental modification on the taxonomic interpretation of selected Antarctic moss species. J. Hattori Bot. Lab. 55: 273-279.

Seppelt, R. D., Green, T. G. A., Schwarz, A. M., and Frost, A. 1992. Extreme southern locations for moss sporophytes in Antarctica. Antarct. Sci. 4: 37-39.

Shirasaki, H. 1984. Ecological distribution of *Bryoxiphium norvegicum* subsp. *japonicum*. J. Phytogeogr. Tax. 32: 59-67.

Shirasaki, H. 1987. Ecological distributions of *Bazzania trilobata* S. Gray and *B. yoshinagana* Hatt. (Hepaticae). Soc. Stud. Phytogeogr. Tax. 35(1): 27-35.

Shirasaki, H. 1996. Distribution and ecology of *Ricciocarpos natans* in Niigata Prefecture and its adjacent regions, central Japan. Proc. Bryol. Soc. Japan 6(11): 209-215.

Shirasaki, H. 1997. Distribution and ecology of *Dichelyma japonicum* in the deep snow-covered district of Niigata Prefecture and its adjacent regions, central Japan. Bryol. Res. 7(2): 44-49.

Shirasaki, H. 1998. Distribution and ecology of *Trachycystis flagellaris* and *T. microphylla* in Niigata Prefecture and its adjacent regions, central Japan. Bryol. Res. 7(5): 139-145.

Slack, N. G., Duckett, J. G., and Capers, R. S. 2013. Monitoring alpine bryophytes and snowbed communities in Northeastern United States. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.

Stark, L. R. 2001. Widespread sporophyte abortion following summer rains in Mojave Desert populations of *Grimmia orbicularis*. Bryologist 104: 115-125.

Stark, L. R. 2005. Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss *Crossidium crassinerve*. J. Bryol. 27: 231-240.

Thomas, W. 1981. Entwicklung eines immissionsme b systems fur PCA, chlorkohlenwasserstoffe und spurenmetalle mittels epiphytischer Moose - angewandt auf den Raum Bayern. Bayreuther Geowiss. Arb., 142 pp.

Trynoski, S. E. and Glime, J. M. 1982. Direction and height of bryophytes on four species of northern trees. Bryologist 85: 281-300.

Ueno, T., Imura, S., and Kanda, H. 2001. Colony form and shoot morphology of *Sanionia uncinata* (Hedw.) Loeske growing in different water conditions in the high Arctic, Spitsbergen, Svalbard. Bryol. Res. 8: 1-6.

Woolgrove, C. E. and Woodin, S. J. 1994. Relationships between the duration of snowlie and the distribution of bryophyte communities within snowbeds in Scotland. J. Bryol. 19: 253-260.

Woolgrove, C. E. and Woodin, S. J. 1996. Effects of pollutants in snowmelt on *Kiaeria starkei*, a characteristic species of late snowbed bryophyte dominated vegetation. New Phytol. 133: 519-529.